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A SURVEY OF THE HAWAIIAN LAND FLORA

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(WITH FIVE FIGURES)

The Hawaiian Archipelago has long been known to the scientific world as a peculiarly isolated island world with many extraordinary biological features. The remoteness of the group from continental areas, the exclusively volcanic nature of the mountains, the extreme specialization of many plant and animal forms—these and many other unique conditions have given particular interest to the biological problems of Hawaii (fig. 1).

It is the purpose of this paper to make a rapid survey of the prominent characteristics and elements of the Hawaiian land flora.[1] The timeliness of such a survey is evident to all who have followed the researches of recent years in the various departments of natural science, as these studies have in many instances necessitated extensive revision of previous records. In order to compress the material within reasonable bounds, much interesting detail is necessarily omitted, and numerous problems of great interest from the standpoint of philosophical biology[2] can here be accorded only passing mention.

[1] For purposes of convenience all of the algae and fungi except the conspicuous woody and fleshy forms are excluded from this consideration of the land flora.

[2] Undoubtedly, after the systematic work on the various groups comprising the Hawaiian fauna and flora has been brought to a stage of comparative completeness, the greatest contributions will be made in the field of philosophical biology. Some of these contributions are suggested in the sections on endemism and precinctiveness in this paper.

For an account of the physical aspects of the Hawaiian Islands, their topography, climate, volcanoes, soils, and geological history, all of which have important and complicated relations with the flora, the reader is referred to such standard treatises as BALDWIN'S *Geography of the Hawaiian Islands*, BRYAN'S *Natural history of Hawaii*, HITCHCOCK'S *Volcanoes of the Hawaiian Islands*, and the excellent article on Hawaii in the latest edition of the *Encyclopedia Britannica*.

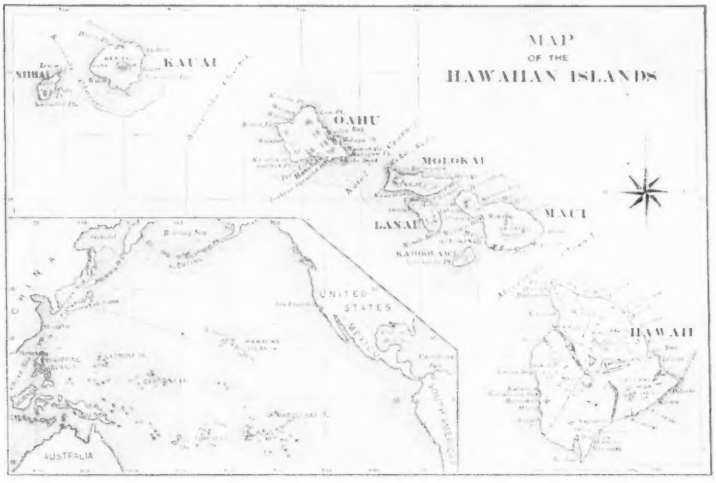

FIG. 1.—Map of the larger islands of the Hawaiian Archipelago

Endemism

A few quantitative statements will elucidate the remarkable endemism of the Hawaiian land flora. There are approximately 1200 species of native plants, exclusive of algae, fungi, and bryophytes. This is also exclusive of the 25, more or less, brought in by the primitive Hawaiians, and discussed later in this paper. Of this number about 200 have been introduced and established within historic times, leaving about 1000 genuine indigenous species. Approximately 700 of these are endemic, thus constituting 70 per cent of the vascular land flora. Restricting the

calculation to "flowering" plants alone, it is estimated that *more than 85 per cent* are endemic. This is a proportion unequaled in the annals of geographical botany. It is particularly significant when compared with the 34 per cent of Samoa, 35 per cent of Tahiti, and 53 per cent of Fiji.

New Zealand, with a land area of 100,000 sq. m., 16 times that of Hawaii, has no more species of flowering plants than Hawaii, and its percentage of endemism, about 75, is markedly lower. Japan, with a total area of 175,000 sq. m., some 28 times that of the Hawaiian Archipelago, has but 1500 species of flowering plants, only 300 more than Hawaii. There is no other region on the earth, of similar area, with so large a list of endemic forms as Hawaii.[3]

In addition to the native flora proper, there are probably 1000 additional species in cultivation or semicultivation in the plantations, ranches,[4] gardens, nurseries, and fern and orchid houses of Hawaii. These have been gathered from all parts of the world, with a natural emphasis upon tropical and subtropical species.

The lucid and comprehensive statement of PERKINS, the eminent student of Hawaiian zoology, is pertinent at this point.

> A comparative study of the many groups of animals represented in the islands, and of the affinities of species to species, and genus to genus, in the groups of allied forms, has led me to believe in the extreme rarity of a successful immigration from outside. The extraordinary gaps in the fauna of whole families of wide distribution, and containing countless species, many of which no doubt would, and some of which after introduction by man are known to thrive in the islands, show clearly how hardly and rarely have immigrants reached them from outside. A limited number of birds and insects, species of well known migratory habits, for which no seas are impassable, doubtless arrive continuously, but these, only in the event of such migration ceasing, are likely to produce new and endemic forms.
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> The phenomena exhibited by the flora appear to me to be extremely similar to those of the fauna. There may be seen the same notable absences

[3] See LYDGATE, The endemic character of the Hawaiian flora. Thrum's Hawaiian Annual. 1911 (pp. 53–58).

[4] Extensive areas on Hawaii, Maui, and Molokai, for example, aggregating hundreds of square miles, are overrun with introduced ranch grasses. These form a dense continuous sod, which not only drives out the native grasses and herbs, but also prevents the germination of seeds of the forest trees and other native plants.

of forms widely distributed elsewhere, the same multiplication of allied species of many of the genera that are present, the same groups of allied genera, embracing many species. I believe that the explanation of these facts is quite in accordance with that which I think to be true of the fauna, as above stated. . . . . The present Hawaiian fauna is derived from waifs and strays from all directions. At rare intervals from the Eocene till now chance immigrants have arrived. Some have been able to establish themselves, many more probably, even after a landing had been effected, have failed. Those that have been successful and have found congenial conditions have often thriven amazingly, giving rise to hosts of descendant species, as they have become adapted to or become modified by diverse conditions. . . . . Where conditions have proved favorable and remained so, and plant or animal has become adapted to special conditions, an exuberance of distinct forms has sprung from the ancient immigrant. Such cases are manifest in the Lobeliaceae amongst plants, and in many groups of animals, the Drepanididae (birds), Plagithmysidae (insects), Achatinellidae (mollusca), and many others. Such form the chief and most interesting part of the native fauna and flora of the present day.[5]

Precinctivity

A second notable feature of the flora is the highly precinctive ranges of many species and varieties. This sharply defined localization of habitat has reached a very advanced stage with many forms. The condition is closely analogous to the equally remarkable precinctive distribution of the arboreal snails (Achatinellidae), and many of the native birds and insects, and is undoubtedly due to the same environmental and evolutionary factors.

The statement may be made conservatively that a very large percentage of the endemic Hawaiian plants are closely confined within areas of a few square miles, and in many instances of a few square rods.[6] Thorough botanical explorations of the past few

[5] From PERKINS' introduction to the *Fauna Hawaiiensis*, being the land fauna of the Hawaiian Islands; by various authors; published in 6 parts, 1899–1913. Cambridge University Press. It may be remarked that endemism is strongly exhibited among the Hawaiian lizards, crabs, holothurians, madreporarians, and various marine groups. See also GULICK, JOHN T., Evolution, racial and habitudinal. Carnegie Inst. Washington. 1905, especially pp. 1–5, dealing with endemism of Hawaiian land shells.

[6] MACCAUGHEY, V., Precinctive flora of the Waianae Mountains. Hawaiian Forester **13**:85–89. 1916; and *Gunnera petaloidea* Gaud. Amer. Jour. Bot. **4**:33–39. 1917.

years have failed to disclose new habitats or localities for many of these precinctive plants. For example, *Drosera longifolia* occurs only in the summit bogs of Kauai; *Pelea pallida* is limited to Kaala, in the Waianae Range; many of the lobelias, cyrtandras, and kaduas are sharply precinctive; *Lagenophora mauiensis* occurs only in the Eeka swamps; and 40 or 50 other well defined illustrations might be cited.[7]

The limitations of this paper forbid any extensive discussion of the remarkable geological history of the Hawaiian Archipelago, and the bearing of this history upon the development of the land flora.[8] It is sufficient to state that the older islands lie to the westward, and that the eastern end of the chain comprises the youngest elements of the group. Many years ago HILLEBRAND noted the contrast between the vegetation of Kauai and Mauna Loa as two extremes. He stated that "the Kauai species of the leading Hawaiian genera are in all instances the most specialized, to be distinguished by more striking characters than the others. Examples are *Schiedea*, *Raillardia*, *Dubautia*, *Campylotheca*, *Lipochaeta*, *Pittosporum*, and *Pelea*. The proportion of species peculiar to Kauai with species peculiar to all the other islands is about 67:382, or 17.5:100."

The studies and explorations of succeeding botanists have tended to confirm and intensify this contrast. Kauai, Waianae on Oahu, the east end of Molokai, West Maui, Kohala and Puu Waa-waa on Hawaii, these are regions much more ancient than the land areas with which they are immediately connected, and their vegetation gives abundant evidence of their antiquity. During the summer of 1916 Professor W. A. BRYAN, of the college of Hawaii, made explorations on the summits of the high mountains of Hawaii which gave abundant and conclusive evidence of a former period of glaciation. His notable discoveries add to the

[7] MACCAUGHEY, V., Vegetation of the Hawaiian summit bogs. Amer. Bot. 22: 45–52. 1916.

[8] The geological researches of recent years have demonstrated that the islands are by no means simple in structure, as was once believed, but on the contrary show innumerable evidences of prolonged and profound geological changes. The complexity of these changes has only lately been fully appreciated, and their unraveling will require painstaking research for many years to come.

accumulating data which point to the great antiquity of this archipelago and to its complex geological history.

Extinction

The flora of today strikingly illustrates the profound biological changes concomitant with the coming of foreigners[9] and the spread of their industries. Practically all of the arable lowlands have been converted into plantations, and are covered with sugar cane, pineapples, and other crops. The level uplands have become sheep and cattle ranches. Agriculture has wiped out practically all the native vegetation in all of these utilizable regions, and the indigenous flora is now largely confined to the mountains and the waste lands.

Feral and semi-wild goats, sheep, swine, and cattle have been the most serious and persistent foes of the native flora. For over a century they have roamed almost unchecked through the forests, overrunning the mountainous districts, and in some instances whole islands. They have totally destroyed or irreparably damaged untold quantities of indigenous vegetation. Many districts have been stripped of all save the weediest and least edible of plants. Some of the smaller islands (Niihau, Lanai, and Kahoolawe) that have long been overstocked with these herbivorous vandals have been depleted almost wholly of the original native flora. The destruction of the vegetative protective covering has exposed these regions to the full force of erosion by wind and water, and this has resulted in the removal of huge quantities of surface soil.

It is difficult to conceive the transformations wrought in the Hawaiian forests by man[10] and his live stock, so extensive have been the devastations. Many herbaceous species have undoubtedly been totally exterminated. Some of the woody species that have become extinct within historic times, or are now on the verge of

[9] Foreigners, that is, others than native Hawaiians; especially Americans, British, Germans, etc.

[10] In the early days the woodlands in the vicinity of the numerous sugar mills and plantations were cut to supply fuel for the mills, and for the plantation villages. The latter use continues to the present time, and there is a serious shortage of firewood on all the islands.

extinction, are *Neowawraea phyllanthoides*, *Alectryon macrococcus*, *Alphitonia excelsa*, *Hibiscadelphus Giffordianus*, *H. Wilderianus*, *H. hualaliensis*, *Kokia Rockii*, *K. drynarioides*, *Clermontia haleakalensis*, *Cyanea arborea*, *C. comata*, and *Hesperomannia arborescens*.

It may be estimated conservatively that probably several hundred species of angiosperms have become extinct since the first landing of live stock on these islands. PERKINS has estimated that 300 species of native insects have been exterminated. The extinction of many of the highly specialized avian species is a lamentable and widely known fact. On the island of Oahu, for example, there are more extinct species of endemic birds than existing species. Numerous forms of the arboreal snails are now excessively rare.

Ocean currents

Hawaii is so remote from other land areas, and is so situated with reference to the great trans-Pacific ocean currents, that comparatively few plants have been added to her flora through the agency of water borne seeds. The shores and beaches present a striking contrast to the forested littoral of many South Pacific Islands, which have been well stocked with plants by the currents.[11]

Logs of coniferous species are thrown upon Hawaii's windward shores after a long drift from the northwest coast of America. These have probably brought seeds and spores in their crevices, although there is no conclusive evidence on this point.[12] BRYAN'S hypothesis is very suggestive in this connection. "It is possible that in bygone ages, long ago, the movements of the Pacific may have been reversed, so that various plants from the Australian, Polynesian, and South American regions that are well known here, might have been carried to the islands by them, in one way or another."

Some of the species that very probably have been introduced by ocean currents are *Scaevola Lobelia*, *Heliotropum curassavicum*,

[11] Seeds of the following woody species are common in the drift material along the beaches: *Aleurites moluccana*, *Calophyllum Inophyllum*, *Terminalia Catappa*, *Mangifera indica*, *Cocos nucifera*, *Thespesia populnea*, *Pandanusodo ratissimus*.

[12] See WARMING, E., Botany of the Faroes. Copenhagen. 1903 (Vol. 2, pp. 660–681; particularly pp. 674–678, on plant immigration across the sea).

H. anomalum, *Vitex trifolia*, *Ipomoea pes-caprae*, *I. acetosaefolia*, *I. bona-nox*, *I. tuberculata*, *Vigna lutea*, *Mucuna gigantea*, *Batis maritima*, *Sesbania tomentosa*, *Capparis sandwichiana*, *Erythrina monosperma*, *Ruppia maritima*, *Colubrina asiatica*, *Dioclea violacea*, *Strongylodon lucidum*, *Caesalpinia Bonducella*, *Cassytha filiformis*, and numerous grasses and sedges.

HITCHCOCK cites *Pandanus* as a typical current disseminated plant.

> A good illustration of the origin of the vegetation is the screw pine, *Pandanus*, or lau hala. . . . . These seeds will stand saturation in water for months without losing their vitality. Hence they may be carried hundreds or thousands of miles from the place of their nativity, and when washed inland by unusually high waves will be placed where they will sprout and grow up. I once saw a place in Kauai where hundreds of young lau halas had started to grow near the seashore. . . . . There is no tree with wider range in the Pacific than the *Pandanus*. And it was in existence in the Triassic period in Europe. It is therefore one of the oldest and most persistent of plants, and the one best fitted to start plant life on the isolated volcanic islands for the first time peering above the waves.[13]

Duration of migration

The philosophical presentation of the status of Hawaiian plant immigrants with reference to the evolution of endemic forms has been made so comprehensively by PERKINS that an extract from his statement is given here.

> Although endemicity of plant or insect, as represented by great peculiarity of structure and usually by the occurrence of numbers of allied species, naturally indicates a very ancient occupation of the land by their immigrant ancestors, yet it does not necessarily follow that paucity of species or the apodemicity of a genus denotes a comparatively recent immigration. A classification of the flora, as belonging to a definite age or era, based on such a supposition will certainly prove erroneous. It is not probable that all immigrants that arrive and become established are able, even after vast time, to become adapted to such diverse conditions as others, and some doubtless are much more slow to do so than others.
>
> The evolution of new genera or species would proceed in a very different manner in different cases. In judging the length of time that any particular

[13] It is quite possible that the *Pandanus* was first brought to the islands by the ancient Hawaiians, from their home in the South Pacific, where this tree is abundant; see concluding section of this paper. Also see GATES, F. C., The pioneer vegetation of Taal Volcano. Philippine Jour. Sci. **9**:391–434. *pls. 8.* 1914.

plant or group of allied plants has existed in the islands, the botanist would be well advised to consider the fauna that is especially attached to these. When one considers that trees little modified from foreign species, for example, *Acacia koa* or *Sophora chrysophylla*, possess a great endemic fauna, not only species, but even genera of birds and insects, quite restricted to or dependent on them, and that some of these creatures are certainly themselves not less remarkable in their peculiarities than the most peculiar of the composites or lobelias, we may hesitate to attribute such plants to a later era than many other elements of the flora, which at first sight appear far more ancient.

Again, while in the islands an abundant endemic fauna restricted to a plant indicates an ancient occupation by the latter, the absence of such a fauna does not necessarily imply the reverse. In a fauna of comparatively few types it may happen that few or no species have reached the islands that could become adapted to certain elements even after great length of time. I think that those who are in favor of the comparatively frequent accession of immigrants to account for the great series of allied species, or groups of allied genera, hardly make full allowance for the great age of the islands. HITCHCOCK remarks in writing of the most recent portion of the group, the still active Mauna Loa on Hawaii, when one considers how little the bulk of the mountain is made up of the few flows delineated on the map, and how small a portion of the whole mass these can be, he is overwhelmed by the certainty that there were millions of streams and that millions of years must be assumed in order to say how old the mountain is. It must have commenced to build up long before the Tertiary period. And here he is considering the most recent portion of the group, and not the vastly more ancient parts.[14]

It is significant that the gymnosperms are entirely absent from the native Hawaiian flora; cycads and conifers have been introduced in recent years.

Zonation

In the Hawaiian Archipelago the large ecological zones are well defined. Elevation above sea level and precipitation are the two dominant factors which determine the local phytogeography. The zonal distribution of the endemic and indigenous vegetation is very pronounced; a very general statement may be made to the effect that the flora perceptibly changes in kinds and quantities of species with every 1000 feet of ascent (figs. 2–5). The following synopsis of the chief zones will serve to indicate the important phytogeographic areas:

[14] See also SCHIMPER, A. F. W., Die Indo-Malayische Strandflora. Jena. 1891.

1. Littoral.—(*a*) *Humid littoral*, along the windward coasts; (*b*) *arid* or *semiarid*, along leeward coasts and coasts far removed from the mountainous interior.

2. Lowlands.—Up to 1000–1500 ft., with humid and arid sections, depending upon relation of topography to trade winds and distance from interior mountains.

3. Forest zone.—(*a*) *Lower forest* (1000–2000 ft.), with humid and arid sections; in early times this zone extended much farther seaward on the various islands than it does now; (*b*) *middle forest*

FIG. 2.—View from a dividing ridge between 2 long humid valleys, looking toward the head of Kau-kona-hua Valley; fog-covered summit ridge, elevation 2300 ft., seen in distance; entire region covered with dense and unbroken rain forest; on slopes and ridges trees average 15–30 ft. in height, in valley and ravines they rise to 40–60 ft.; annual precipitation at head of this valley approximates 200–300 inches.

(1800–5000 ft.), range variable, with humid and arid sections; this comprises in the humid areas the typical Hawaiian rain forest, highly hygrophytic and very rich in endemic forms; (*c*) *upper forest* (5000–9000 ft.), restricted to the high mountains of Maui and Hawaii.

4. Summit regions.—(*a*) *Xerophytic summits* (9000–14,000 ft.); high mountains of Maui and Hawaii; (*b*) *hygrophytic summits* (4000–6000 ft.); peaks rising into the cloud zone, with summit bogs.

Palms

The palms furnish an interesting illustration of the 3 floral elements: indigenous, native introductions, and modern introductions.[15] The capital city, Honolulu, is a veritable palm garden; there are some 80 species represented, which have been gathered from all parts of the tropics. There is scarcely a home or yard without its palms; some of the finest driveways are colonnaded with such stately species as *Oreodoxa regia* and *Phoenix dactylifera;*

FIG. 3.—Arid, deeply eroded summit ridge, elevation 2000 ft., of eastern Koolau Mountains; absence of vegetation due partly to aridity, partly to devastations of goats; remnants of original forest cover occur here and there in hanging valleys near sky line and in deep ravines.

and certain of the old estates, the famous Hillebrand gardens for example, are crowded with rare and choice specimens. The only palm introduced by the natives (and this introduction is necessarily more or less theoretical, in the absence of historical records) was the coco palm. This species (*Cocos nucifera*) is widely spread throughout Polynesia, and in early times formed a characteristic feature of many Hawaiian shores and beaches.

[15] MACCAUGHEY, V., The economic woods of Hawaii. Forest Quarterly **14**: 696–716. 1916.

The indigenous palms are confined to the single genus *Pritchardia*, and are all endemic. There are a number of Hawaiian species, perhaps a dozen. The exact botanical status of these has not as yet been fully determined. The species of *Pritchardia* occur mainly in the rain forests and along exposed humid summit ridges. They are scattered, are usually solitary or in small clumps, never form pure stands, and constitute a very minor element in the forest. From the standpoint of abundance or striking features,

FIG. 4.—Xerophytic promontory, Ka-ena Point, a typical "dry ridge" formation; other similar ridges, separating arid valleys, seen to the right; in foreground a coral beach formation covering ancient lava beds; note stratification of lava flows in the faces of promontory, also extensive talus slopes.

the native palms are as disappointing as the native orchids. They occasionally attain considerable height (40–50 ft.), but are customarily of short or even dwarf stature. *Pritchardia* is confined to the islands of the Pacific. The Hawaiian species show close affinities with those of the South Seas.

Many of the other monocotyledonous families are but meagerly represented. The Orchidaceae, for example, that attain unrivaled

luxuriance and marvelous specialization in many tropical regions, have only 3 species in Hawaii, and these are all shy, poor, homely little plants.[16] *Pandanus* is represented by one species, formerly abundant in the lowlands. *Freycinetia Arnotti* Gaud. is a tall woody liana, common in the lower forest zone of all the islands, and often forming dense jungles.

The liliaceous plants of Hawaii are in part woody species; none are bulbs, and none have particularly showy flowers. Of the

FIG. 5.—Lava flow of the smooth or "pa-hoe-hoe" type; shows invasion by lichens and ferns; in arid situations lava flows retain a new, fresh appearance for a long period of years; under humid conditions they rapidly disintegrate and are soon covered with plant life.

5 genera, 3 are monotypic: *Cordyline terminalis*, a tall shrub; *Dracaena aurea*, a tree; and *Dianella odorata*, a large herbaceous perennial; all are abundant. *Astelia* and *Smilax* are confined to the forest and upper zones, and none of the group occur on the coastal plains or lowlands. There are no "fields of lilies" in Hawaii. *Commelina nudiflora* is exceedingly abundant in moist

[16] MACCAUGHEY, V., The orchids of Hawaii. Plant World **19**:350–355. 1916.

situations throughout the lowlands, forming pure stands and smothering other vegetation.

The large and highly diversified tropical order of the aroids has no place in the Hawaiian flora, except 2 naturalized species, *Colocasia* and *Alocasia*, introduced by the ancient Hawaiians. *Colocasia antiquorum*, the kalo or taro, was the staple food of the primitive Hawaiians. The plant was raised both in irrigated fields (*loi*) and on the uplands (*Kula*). *Alocasia macrorrhiza*, the ape or giant taro, was raised in clearings in the lower forest, and used chiefly in time of famine. Ornamental aroids of many genera are now abundant in Honolulu gardens, but these are strictly exotic, and none of these are naturalized.

Another group that one naturally associates with a tropical background is the Begoniaceae, and yet of the 400 species, only one is native to the Hawaiian Archipelago. Our lone species is endemic, and is so distinct from its relatives that it has been placed in a monotypic genus, *Hillebrandia*. It is a beautiful plant with ornamental foliage and fine showy clusters of pink flowers, but is limited to such isolated and difficult regions that few people, either natives or whites, have seen it.

Lobelias

Unquestionably the crowning glory of our flora are the arborescent lobelias. These constitute one of the unique elements of the Hawaiian forest flora, and aggregate some 100 species, distributed among 6 genera, 5 of which are endemic. As ROCK[17] succinctly states, "nowhere in the world does this tribe reach such a wonderful development in such a comparatively small area."

The lobelias surpass in number of species all other plant families comprising the Hawaiian land flora. Many of the species show extreme specialization. The extraordinary range of variation strongly suggests that we are witnessing the last spasmodic outbursts of the evolutionary impetus of this group. Quite unlike the small herbaceous lobelias familiar on the continent, all of our species have stout woody stems. The majority are tall shrubs or

[17] ROCK, J. F., Synopsis of the Hawaiian flora. Thrum's Annual, Honolulu. 1912 (pp. 82–91).

trees, and some reach the amazing height of 40 ft. Many species have a slender, naked, palmlike trunk, closely marked with conspicuous leaf scars. This pole terminates in a large rosette of foliage and a showy inflorescence. These and other characters give the plant a deceptively primitive aspect.

The Hawaiian genera are *Brighamia*, endemic, 1 species; *Lobelia*, 5 endemic species; *Clermontia*, endemic, 17 species; *Rollandia*, endemic, 6 species; *Delissea*, endemic, 7 species; *Cyanea*, endemic, about 45 species. There are many features, both structural and ecological, which strongly suggest that our lobelias are the remnants of a very ancient flora, a flora that has well nigh been obliterated by profound geological and climatic changes.

It is significant to observe that the other islands of the Pacific are practically lacking in lobelias. Furthermore, in other parts of the world these plants are notably alpine in distribution. Many high mountains of the tropics and subtropics are marked by a lobeliaceous flora similar to that of our Hawaiian mountains. These and other facts in local phytogeography lean strongly toward the geological hypothesis that at one time these island mountains stood at a much higher level (perhaps thousands of feet higher) above the sea than at present. Under this theory the islands as they now stand are but the vestiges of a former extensive land mass.[18] PILSBURY uses this hypothesis to explain the extraordinary geographic distribution of the Hawaiian arboreal mollusks. It undoubtedly has an application to such phytogeographic problems as are involved in any attempt to elucidate the origin of the Hawaiian lobelias.

Cyrtandras

One of the largest of the Hawaiian genera, and notably rich in endemic species and varieties, is *Cyrtandra*. The genus ranges throughout the islands of the Indian and Pacific oceans and in China, with a total of about 200 species. Of the 30 or more Hawaiian species, all are soft-wooded shrubs, and practically all are endemic. The remarkable variability of the genus is manifest

[18] HILLEBRAND, WILLIAM, Flora of the Hawaiian Islands. 1888; published posthumously; out of print for many years; the standard flora of the islands, although now in serious need of taxonomic revision.

to a high degree by many of our species. As HILLEBRAND states, "the polymorphism of the Hawaiian cyrtandras is extraordinary; no single form extends over the whole group, and not many are common to more than one island. The variations affect every part of the plant, and branch out and intercross each other in manifold ways to such an extent that it is next to impossible to define exact limits of species."[19] The evolutionary status of our species is closely analogous to that of the native lobelias.

The species of *Cyrtandra* are largely confined to the humid regions; they are precinctive and extremely shade-tolerant. Many species are to be found only in the narrow-walled ravines and dimly lighted recesses of the rain forest. *C. cordifolia* Gaud., *C. Pickeringii* Gray, *C. gracilis* Hbd., *C. Kahilii* Wawra, *C. grandiflora* Gaud., *C. paludosa* Gaud., *C. latebrosa* Hbd., and *C. Lessoniana* Gaud. are representative Hawaiian species of this genus.

Composites

Second only to the lobelias in importance are the Compositae. There are over 80 species, representing 29 genera; of these, 60 species are distributed among 9 endemic genera. Several of the genera (*Argyroxiphium*, *Wilkesia*, *Hesperomannia*, and *Remya*) show many evidences of isolated and specialized evolution and, as HILLEBRAND remarks, "probably belong to the oldest denizens of our islands, a supposition countenanced by the fact that each holds no more than two species." With reference to the last statement it must be remarked that several new forms in these groups, probably of specific rank, have recently been discovered.

A number of these peculiar Compositae (*Artemisia*, *Dubautia*, *Raillardia*) are arborescent, and alpine in habitat. On the high mountains of Maui and Hawaii they reach an elevation of 10,000 feet. *Lagenophora* is a peculiar summit bog form.

To this family belongs one of the most famous of Hawaiian plants, the beautiful silver sword (*Argyroxiphium sandwicense*). This plant has a large, compact basal head of dagger-shaped leaves

[19] WINNE, W. K., Intercontinental land connections and their relations to plant migrations. Chicago. 1914 (p. 24, "The Pacific continent").

densely covered with shining silvery pubescence; from this body arises a tall inflorescence (6–8 ft.) of showy purple flowers. This unique herbaceous perennial is xerophytic, and occurs only at high elevations on Maui and Hawaii.

Lipochaeta, *Coreopsis*, and *Tetramolopium* are large genera of herbaceous or semiligneous perennials; there are 10 or 12 species in each genus, mostly endemic. The flowers are small, but very numerous, and form showy masses of rich yellow. *Bidens*, *Ageratum*, *Xanthium*, *Sonchus*, *Vernonia*, *Erigeron*, *Gnaphalium*, *Franseria*, *Eclipta*, and *Centaurea* are common weeds of the roadsides and fields.

Modern research in ornithology has demonstrated the existence of several bird migration routes from South America to the north via Hawaii. The Hawaiian goose and the Pacific golden plover furnish specific instances of these long over-sea migrations. Inasmuch as a number of the endemic composites show close affinity with certain Andean and other South American species, it is highly probable that they were carried thither by migrating birds.[20]

A number of other native plants were probably brought by the same agencies, for example, *Rubus*, several endemic species, closely related to Pacific Coast forms; *Nertera depressa*, with fleshy red drupes, a South Pacific Coast species; *Fragaria chilensis*, which also occurs along Pacific America; *Dodonea viscosa*, with glutinous capsules, and widely dispersed; *Lycium sandwicense*, and others.

Leguminosae

The vast family Leguminosae, rivaled in size and distribution only by the Compositae, is abundantly represented in our flora. There are nearly 30 genera, many of comparatively recent introduction, but now well and widely established. Four genera, *Acacia*, *Sophora*, *Mezoneurum*, and *Erythrina*, are arborescent. Endemic species occur in *Vicia*, *Canavalia*, *Vigna*, *Acacia*, *Mezoneurum*, and *Sophora*. There are many introduced leguminous plants in Honolulu; particularly conspicuous are the flowering

[20] See ERNST, A., The new flora of the volcanic Island of Krakatau. Trans. by SEWARD. Cambridge. 1908 (pp. 58–60, "Seed-dispersal by birds").

trees of *Cassia*, *Poinciana*, *Peltophorum*, *Pithecolobium*, and allied genera.[21]

A number of the indigenous legumes are beautiful, high-climbing woodland vines, with showy clusters of bright colored flowers; *Syrongylodon lucidum*, *Vicia Menziesii*, *Mucuna urens*, *Dioclea violacea*, and *Canavalia galeata* are examples of these. Species of *Crotalaria*, *Indigofera*, *Leucaena*, *Acacia*, *Mimosa*, *Dolichos*, *Medicago*, *Phaseolus*, and *Desmodium* are common roadside weeds. The most valuable and widely known of our cabinet woods, *koa*, is from the common forest tree *Acacia koa*.

Rubiaceae

The Rubiaceae comprise a large and diversified portion of our flora. There are 13 genera, of which 4 (*Kadua*, *Gouldia*, *Bobea*, and *Straussia*) are endemic. There are between 50 and 60 rubiaceous species; of these the majority are tall shrubs or arborescent. The other genera (*Gardenia*, *Plectronia*, *Coffea*, *Morinda*, *Psychotria*, *Paederia*, *Nertera*, *Coprosma*, and *Richardsonia*) occur in many other tropical regions.

Of special interest, because of their beautiful flowers, are the two endemic species of *Gardenia*. The blossoms are large, white, deliciously fragrant, and rank high among the wild flowers of Hawaii. The coffee (*C. arabica*) was introduced in 1823, and its cultivation spread rapidly to all of the larger islands of the group. Although a combination of economic and cultural factors has largely suppressed the coffee industry, the plant itself is thoroughly naturalized, and occurs in many of the humid lower regions. Birds have undoubtedly assisted in its dissemination.

Rutaceae

Rutaceous trees and shrubs comprise a conspicuous and abundant element in the native forests. There are few groves or wooded slopes that do not contain a generous proportion of rutaceous

[21] The algaroba or mesquite (*Prosopis juliflora*) was introduced nearly a century ago, and has become widely spread through the agency of cattle. Today it is one of Hawaii's most valuable trees, and is abundant on the lowlands to the 2000 foot contour. It is an important source of honey, nutritious pods, and firewood, and greatly ameliorates the soil upon which it grows.

species. Two of the three genera (*Pelea* and *Platydesma*) are endemic; the third (*Zanthoxylum*) is world wide in its range. *Pelea*, named in honor of the Hawaiian volcano goddess Pele, is a large genus, with nearly 30 recognized species and an even larger number of varieties. Like the species of *Cyrtandra* and the lobeliaceous genera, the species of *Pelea* are highly variable, with many intergrading forms, so that as yet the species are poorly defined.

Platydesma is an isolated genus, with 4 woody species. *Zanthoxylum* has 7 species, 6 arborescent, and many varieties. The majority of these are characteristic of arid leeward regions and old lava flows. There are no native citrus fruits, although the orange has become naturalized in many districts, particularly in the Kona district, on Hawaii.

Violaceae

The endemic Violaceae are a distinct surprise to the mainland botanist on his first excursions in our Hawaiian forests. Instead of tender little herbs, he finds stout woody shrubs, ranging in height from 3 to 6 ft. The flowers are quite like those of the familiar eastern violets, and are white, pink, purple, or blue in color, according to species. There are 7 or 8 species, ranging in habitat from hot, exposed, semiarid regions to the cold, rain-soaked summit bogs. They occur on all the islands, and in certain favorable localities, as the Molekai swamps, they cover considerable areas.

Several species, for example *V. helioscopa*, have large showy flowers of great beauty and fragrance, and suggest novel horticultural possibilities in the way of cultivated violet bushes. Undoubtedly, as familiarity with the native flora increases and methods for transplanting and culture are improved, some of these lovely shrubs will be utilized in horticulture.

Araliaceae

This large and widely distributed family is prominent in the Hawaiian flora. All of our species are trees, and many of them form a conspicuous feature of the xerophytic woodlands, inhabiting the barren lava fields and other arid regions. The Araliaceae had two great centers of distribution, tropical America and Malaya.

It is probable that Hawaii originally received its contribution from the Malayan center, although its 4 genera are now almost wholly endemic.

All of the 13 or more Hawaiian species are endemic, and of these a number are sharply localized in their range. The 4 genera are represented as follows: *Tetraplasandra*, 7 spp.; *Reynoldsia*, 1 sp.; *Pterotropia*, 3 spp.; *Cheirodendron*, 2 spp. The characteristic American-Asiatic genera *Aralia* and *Panax* do not occur in Hawaii.

Labiatae

The Labiatae are represented by 7 genera. Three (*Stenogyne* with 16 to 18 species, *Phyllostegia* with about 20 species, and *Haplostachys* with 3 species) are endemic. *Plectranthus* comes from Australia, and *Sphacele* from the Pacific Coast of America. The two remaining genera (*Salvia* and *Stachys*) are weeds of world-wide geographic range.

Hawaii has no equivalent for the familiar mints of eastern fields and waysides, such as catnip, peppermint, pennyroyal, hoarhound, and a score of others. Our *Sphacele hastata*, endemic from an Andean genus, is a typical example of precinctiveness. It forms an extensive belt around the great volcanic mountain Hale-a-ka-la at an elevation of about 3000 ft., and occurs nowhere else in the archipelago.

Many of the shrubby species of *Phyllostegia* and *Stenogyne* have lovely masses of flowers, white, pink, and red, and give beautiful color effects against the dark greens of the rain forest and the wet shadowy jungles which they inhabit.[22]

Malvaceae

The Malvaceae constitute a large family, dispersed over the whole world, except the arctic regions, and richly represented in the tropics and subtropics. Hawaii is well endowed with this group. There are 2 endemic genera: *Kokia*, the Hawaiian tree cotton, with 2 species; and *Hibiscadelphus*, with 3 species. All of these are excessively rare and localized.

[22] MACCAUGHEY, V., The wild flowers of Hawaii. Amer. Bot. **22**:97–105, 131–135. 1916.

The large genus *Hibiscus* has 6 or 7 native species, all shrubs or trees, with large flowers of striking beauty. The blossoms are white, pink, red, or yellow, according to species, and form a distinctive feature of the rain forest.

The cosmopolitan genera *Malva*, *Malvastrum*, *Sida*, and *Abutilon* are common on the semiarid lowlands. *Gossypium*, the true cotton, includes the unique Hawaiian cotton, *G. tomenlosum*, a spreading shrub, endemic, densely covered with white tomentum, and growing in arid situations along the coasts.

Solanaceae

Of the 70 genera of this family, only 3 (*Solanum*, *Nothocestrum*, and *Lycium*) comprise elements in our native flora. There are many introduced Solanaceae (*Physalis*, *Datura*, *Nicotiana*, etc.), some brought in at a very early period and now thoroughly established. The genus *Solanum* has 6 endemic species, one arborescent; in addition to these there are a number of weeds belonging to this genus. *Nothocestrum* is an endemic genus of 4 arborescent species, and is closely related to the Brazilian genus *Athenaea*. *Lycium*, a genus of 70 species, is represented in our flora by a single widely distributed littoral species.

Grasses

The grasses, including many introduced and now naturalized species, have about 40 genera in the flora. None of these are endemic, although there are a number of endemic species. Some of the more important genera, from the standpoint of distribution and number of species, are *Bromus*, *Calamagrostis*, *Cenchrus*, *Chloris*, *Chrysopogon*, *Cynodon*, *Dactylis*, *Eleusine*, *Eragrostis*, *Festuca*, *Heteropogon*, *Holcus*, *Koeleria*, *Lolium*, *Panicum*, *Paspalum*, *Poa*, and *Stenotaphrum*.

The highly developed sugar-cane industry has monopolized most of the arable lowlands, and needs no further comment here. Rice and corn are also raised; in early times wheat, barley, and oats were exported to California, but are now imported. Clumps of *Bambusa vulgaris*, early naturalized, are scattered here and there in the humid valleys. The prevalent lawn grass in Hawaii is the Bermuda grass, *Cynodon dactylon*.

The representation of Cyperaceae is roughly as follows: *Cyperus* 17 spp., *Kyllingia* 1, *Fimbristylis* 4, *Eleocharis* 1, *Scirpus* 2, *Hypolytrum* 1, *Rhynchospora* 4, *Cladium* 1, *Baumea* 1, *Vincentia* 1, *Gahnia* 5, *Oreobolus* 1, *Scleria* 1, *Uncinia* 1, *Carex* 5.

Absent pests

Hawaii is entirely free from any plants poisonous to the touch. To the botanist familiar with the distressing prevalence of these pernicious vines and shrubs in the continental woodlands, it is a relief to work one's way through a Hawaiian jungle with the certainty of complete safety in this regard. Neither are there any stinging nettles. *Mucuna urens*, the well known "cow-itch" plant, whose pods are covered with stinging hairs, is naturalized in certain restricted areas on the islands of Maui and Hawaii.

The Anacardiaceae are represented in Hawaii by a single arborescent Asiatic *Rhus* (*R. semialata* Murray var. *sandwicensis* Engler). This species extends from India and the Orient to Hawaii, and is non-poisonous. Our variety is a small tree, growing in isolated clumps in all the islands.

It is to be hoped that the pernicious *T. vernix*, *T. radicans*, and *T. Toxicodendron* of North America may never by any accident reach Hawaii. The noisome *Paederia foetida* was accidentally introduced a number of years ago, and its seeds, like those of *Rhus Toxicodendron*, are abundantly distributed by birds. It is now a pest in many of the valleys, as it smothers all other vegetation.

Ferns

There are 43 genera and 185 species of pteridophytes; of these, 2 genera and 118 species are endemic. There are 18 genera with all or 75 per cent and over of endemic species; 18 genera possess no endemic species, or have 75 per cent or over of non-endemic species; 33 species are practically cosmopolitan; 8 species have the west coast of America as their chief station; 22 species have the South Pacific as their chief station; and 2 species have the east coast of Asia as their homeland.

The fern flora of Hawaii is rich and diversified. Like the lichens and the mosses, the ferns are to be found in all habitats,

from the arid raw lava flows to the most humid portions of the jungle forest. A number of species (*Cibotium* and *Sadleria*) attain arborescent stature (8–35 ft.) and many others are of large size.[23] The other extreme is found in the minute Hymenophyllaceae. These are abundant in the rain forest, and clothe the trees with their filmy fronds.

There are about 22 genera of true ferns. The largest of these are *Asplenium*, 40 spp.; *Dryopteris*, 21; *Polypodium* 14, *Elaphoglossum* 8, *Diellia* and *Athyrium* 6, *Sadleria* 5, *Trichomanes* 4. The number of species in the larger genera, and in some of the smaller as well, must be stated as approximations, as many of these species are in serious need of revision. Many of the forms hitherto described as varieties will undoubtedly be raised to specific rank upon careful investigation, and numerous specific descriptions require redefinition.

Some of the abundant forms not indicated by the generic list are *Marattia Douglasii*, *Gleichenia* spp., *Gymnogramme javanica*, *Vittaria elongata*, *Nephrolepis exaltata*, *Cystopteris Douglasii*, *Doodya media*, *Odontoloma repens*, *Micropelia* spp., *Schizostegia Lydgatei*, *Pellaea ternifolia*, and *Adiantum* spp. These are all of genera represented by only a few species.

Salviniaceae are represented by a recently introduced *Azolla;* Marsileaceae by 2 endemic species of *Marsilea;* Equisetales are not represented. The Lycopodiales have 3 genera in the flora: *Lycopodium* with 10 spp. and 5 endemic; *Psilotum* with 20 widely distributed species; and *Selaginella* with 3 endemic and 1 other species. About 50 of the Hawaiian pteridophytes are epidendrous; 15 are xerophytic; and about 15 are lithophilous. The great majority inhabit the rain forests at elevations of 1000–6000 ft.

Bryophytes

Mosses are also very abundant, both in dry and humid regions. In the rain forest are many epiphytic species that clothe the trunks and branches with a dense, soggy envelope of greenery. These jungle moss forests are very beautiful. The summit bogs are the

[23] MacCaughey, V., The tree ferns of Hawaii. Amer. Bot. 22:1–9. 1916.

habitats of many mosses, which completely cover the water-saturated ground of large areas, and mask the treacherous quagmire.[24] The liverworts, including the Marchantiales, Anthocerotales, and Jungermanniales, are abundant in the humid regions, many species being epiphytic and epiphyllous. Species of *Marchantia*, *Anthoceros*, and related genera are conspicuous along streamways and in other moist places.

Fungi

The larger fungi are conspicuously absent from the woodlands. There are a few woody brackets, a few dull-colored mushrooms, a few puffballs and trembling fungi. The sum total of all these is insignificant, however, when compared with the rich fungus flora of such a region as the eastern United States. One may gather more fleshy fungi in a day's collecting in New York, for example, than he would find in diligently scouring our forests for a week. This condition is somewhat surprising, as the cool, humid rain forest zone, with its abundance of decaying vegetation, would appear to be favorable for the development of the fleshy fungi. A number of species of slime molds occur in the ravines and jungles. It is to be regretted that no comprehensive study of the Hawaiian fungi has been made.[25]

Lichens are abundant in all parts of the islands. They comprise the first invaders of the freshly cooled lava flows. They luxuriate in the cool humidity of the rain forest and the summit bogs. They cover the exposed cliffs and ledges of the middle zones, and withstand the aridity of the leeward lowlands and of the high mountains (6000–14,000 ft.). The lichen flora not only occupies a wide variety of ecological areas, but furthermore is of considerable richness. No comprehensive statement can be made as to genera and species, as the Hawaiian lichens have never received exhaustive study.

[24] GATES, F. C., A sphagnum bog in the tropics. Jour. Ecology 3: 24–30. *pl. 1. fig. 1.* 1915.

[25] RICHARDS, H. W., Beiträge zur Flora der Hawaiischen Inseln. Vienna. 1878.

BERKELEY, M. J., Description of fungi collected by R. B. HINDS in islands of Pacific. Hook. Jour. 1842.

———, Fungi of the Challenger Expedition. Linn. Jour. 1878.

Aboriginal introductions

Any outline of the Hawaiian flora would be seriously defective that did not give prominence to the numerous plant introductions by the primitive Hawaiians in their migrations from Samoa and the South Seas. Carefully gathered historical evidence has established the fact that during a long period of time, probably several centuries, the ancient Hawaiians maintained intercourse with their kinfolk in the South Pacific, making the long voyages in their splendid canoes. During this eventful period of migration and intercourse with the south, about 25 species of useful plants were consciously introduced by the natives, and perhaps a much larger number unconsciously brought in as seeds and spores. The list includes:[26]

*Colocasia esculenta; the taro; starchy corms used for food.
Ipomoea Batatas; sweet potato; many native varieties.
*Musa sapientum banana; many native varieties.
Artocarpus incisa; breadfruit tree; seedless.
*Cocos nucifera; cocoanut palm; formerly very common.
*Dioscorea sativa; yam; starchy tubers; climbing vine.
*Dioscorea pentaphylla; yam; starchy tubers; climbing vine.
*Alocasia macrorrhiza; giant taro; starchy corms.
*Tacca pinnatifida; arrowroot; starchy rhizomes.
*Jambosa malaccensis; mountain apple tree; delicious fruits.
Saccharum officinarum; sugar cane; several native varieties.
*Cordyline terminalis; ti bush, with sweet, edible roots.
*Piper methysticum; awa vine; famous Polynesian intoxicant.
*Zingiber Zerumbet; wild ginger; common in lower forest.
*Curcuma longa; well known dye plant; yellow rhizomes.
*Aleurites moluccana; kukui or candlenut tree; illuminating oil.
*Calophyllum Inophyllum; kamani tree; shade, wood, and oil.
*Hibiscus tilaceus; hau tree; fiber, wood, and shade.
*Pandanus odoratissimus; hala tree; fiber and food.
*Broussonettia papyrifera; wauke bush; cloth plant of Polynesia.
*Boehmeria stipularis; opuhi bush; fiber plant.
*Thespesia populnea; milo tree; shade and wood.
*Cordia subcordata; kou tree; shade and wood.
Cucurbita maxima; large gourd, for calabashes.
Lagenaria vulgaris; small gourd, for calabashes.

[26] MACCAUGHEY, V., The food plants of the ancient Hawaiians. Sci. Monthly 4:75–80. 1917.

The starred names indicate species that have escaped from cultivation. Many of these have become so thoroughly naturalized and established in the lower forests, on the lowlands, and along the beaches that they are easily confused with the true indigenous flora.

The successful importation of this diversified series of edible, fiber-producing, oil-producing, and other useful plants, from lands so remote, and by methods so primitive, betokens native horticultural skill of no mean importance. As stated by LYDGATE, "the successful introduction, perhaps acclimatization even, must have meant repeated voyages, extending over generations or even centuries. And not time alone, but patience and skill must have been required for the successful introduction of a seedless tree like the breadfruit. Under favorable conditions it is not easy to propagate; exposed to the trying vicissitudes of a long canoe voyage, weeks of wind and weather and open sea, lack of water, burning sun and blighting spray, huddled into the bottom of the shallow canoe, how many, many failures there must have been."

In conclusion, it may be pertinent to suggest that there is an unwritten chapter in the history of Hawaii's introduced flora, namely the introductions possibly made by the early Spanish explorers. They undoubtedly visited the islands repeatedly, long before the discovery by COOK[27]; there are numerous evidences of their intercourse with the natives, and it is not all beyond the realm of probability that some of the plants now thoroughly naturalized were brought in by these early Spaniards.

COLLEGE OF HAWAII
HONOLULU

[27] Historical evidence shows that probably the first Europeans to land on the Hawaiian Islands were shipwrecked Spaniards, in November, 1527. In 1555 they were discovered by the Spanish navigator JUAN GAETANO, over 200 years before the famous discovery by Captain JAMES COOK (1778).

THE GAMETOPHYTES OF TAXUS CANADENSIS MARSH

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 234

A. W. DUPLER

(WITH PLATES XI–XIV)

Introduction

While the European *Taxus baccata* L. has been studied by a number of workers and its morphology is quite well known, up to the present time no accounts have been published dealing in any connected way with the morphology of the American form, *Taxus canadensis* Marsh., records having been made of only a few scattered observations. Although by some, including PILGER (7) in ENGLER'S *Das Pflanzenreich*, *T. canadensis* is considered as merely a subspecies of *T. baccata*, it has seemed worth while to investigate its morphology and compare it with other forms, and especially with the results obtained in the study of *T. baccata*, most of the work in which was done a number of years ago. The present paper gives an account of the male and female gametophytes in connection with other closely related features. Papers dealing with other phases of the morphology will follow.

Material

The material used in this study was collected during the autumn of 1913 and the years 1914 and 1915 at Huntingdon, Pennsylvania, Sawyer, Michigan, and Mount Carroll, Illinois. Chrome-acetic acid was the chief killing agent used, although some material was killed in formalin-alcohol, but on the whole with results less satisfactory than with the chrome-acetic acid. Heidenhain's iron-alum-hematoxylin, safranin with gentian violet, safranin with light green, and sometimes light green as a contrast stain with the iron-alum-hematoxylin were the stains used. The first of these gave the most satisfactory results in most cases, and for most structures.

Historical

Taxus baccata has long been a favorite form for study, the ovule and the seed first attracting attention, and the early work, therefore, relating almost exclusively to these features. The first study of any importance relating to the gametophytes was that of HOFMEISTER (1), who reported some of the more obvious features of both the male and female gametophytes. The history of the male gametophyte has become further known through the work of BELAJEFF (3), STRASBURGER (4), and JÄGER (6). Miss ROBERTSON (18) made some observations, but, in her own words, her "results on the whole simply confirmed previous work." COKER (9) studied the microspores in *T. baccata* and several of its varieties. STRASBURGER'S early work had to do more especially with the ovulate shoot and the ovule, but in 1879 (2) he described the origin of the megaspore mother cells from the hypodermal layer of the nucellus and gave a few observations on the development of the female gametophyte. The best accounts of the female gametophyte are by JÄGER (6), who gave a rather complete description from the megaspore to the mature endosperm, and by STRASBURGER (12), who gave attention particularly to the early stages, especially to the formation of the megaspores and the free nuclear situation. COKER (9) also studied the megaspores.

In *T. canadensis* itself very little work has been reported. HOFMEISTER (1) has a note concerning the proembryo; CHAMBERLAIN (5) studied the condition of the microsporangium at the beginning of October; COKER (9) reports "more than one embryo sac . . . . not uncommon in *Taxus canadensis*"; and THOMSON (15) has studied the condition of the megaspore membrane.

Male gametophyte

MICROSPORES.—CHAMBERLAIN (5) in material of *T. canadensis* Marsh. collected in the Chicago region, October 1, 1897, found the microsporangium in the spore mother cell stage, and this has been reported (20) as the winter condition. Material collected by the writer, October 10, 1913, shows microspore formation, and material collected at later dates from several localities and in different years in all cases shows the microspores already formed. The

sporangium develops during the summer, and by the time mentioned the microspores are forming (figs. 2–12). In a single strobilus all stages from spore mother cells to completed tetrads may be found. Different stages are also found in a single sporangium, although here the range is not so great as in case of the entire strobilus.

Reduction in the chromosome number and the formation of microspores take place as the result of the usual two divisions of the mother cell. The first division (figs. 2–5) results in two hemispherical cells, and this is followed by the second division (figs. 6, 7), usually in the same plane, resulting in the bilateral tetrad of microspores, although the two planes of division may sometimes be at right angles to one another. Sometimes the second divisions are not simultaneous (fig. 8). Further divisions may also occur, resulting in the formation of more than 4 microspores from a single mother cell, as many as 6 having been found (figs. 9–12). The microspores soon separate from one another and become surrounded by moderately heavy spore coats (fig. 13), the tapetum remaining quite prominent and showing little signs of disintegration even at this time. The microspore stage is the winter condition of the microsporangium, the only noticeable change in the microspores between this and pollination being an increase in size (figs. 13, 14). This growth takes place in the early spring, during the period in which the strobilus is emerging from the winter scales and attaining its mature size (about the middle of April).

Torreya californica in England (**10**) and *T. taxifolia* in Florida (**14**) pass the winter in the mother cell condition. STRASBURGER (**12**) reports that in *Taxus baccata* the "pollen mother cells" divided, in 1904, during unusually warm weather in February. So far as reported, *T. canadensis* is the only one of the Taxineae passing the winter in the microspore stage, the microspore mother cell or earlier being the more usual winter condition of our north temperate gymnosperms.

The pollen grain is uninucleate (fig. 14) when shed and shows no indications of prothallial cells, this agreeing with *T. baccata* as reported by several workers (BELAJEFF **3**, JÄGER **6**, and COKER **9**). Among the other Taxineae, *Torreya* (**14**) and *Cephalotaxus* (**4**, **16**,

17) are binucleate when shed, the microspore having divided into the tube and generative cells while in the microsporangium. The absence of prothallial cells is a feature common to the Taxineae, Taxodineae, and Cupressineae.

POLLINATION.—In the spring of 1914, in the vicinity of Huntingdon, Pennsylvania, pollination was first noted April 23. No strobili were found shedding pollen on April 20, but 3 days later pollen was being shed abundantly, especially in the more exposed situations, and most of the ovules collected at that time contain pollen grains. JÄGER (6), at Zurich, reports the beginning or middle of March as the time for the pollination of *T. baccata*.

The pollen grains are wind scattered and are formed in great abundance, while the frequent occurrence of both staminate and ovulate strobili on the same shoot increases the chances for pollination. In the material which I have examined there were very few ovules which had not been pollinated, and sometimes quite abundantly, as is evidenced by the frequency of several pollen tubes in an ovule. The pollen is caught by the small pollination droplet which protrudes from the micropyle of the ovule and is drawn into the micropyle by the concentration of the droplet.

In the ovule the pollen grains are found on the upper end of the nucellus. While no definite pollen chamber is formed, the outermost cells of the nucellus begin to disintegrate about the time of pollination, resulting in a ragged edge to the nucellus on which the pollen grains become lodged.

POLLEN TUBE.—The pollen grain, lying on the nucellus, soon begins to elongate, the exine is ruptured, and the intine grows out to form the tube. The young tube soon penetrates the nucellus, and, once started, invades the tissue very rapidly. Within a week or 10 days some of the tubes have reached the female gametophyte, while others may not have penetrated so far, there being considerable variation in this respect even in a single ovule, although the rapid growth is the more general situation (figs. 16–20, 22).

The general course of the pollen tube is toward the region of the female gametophyte, which occupies the center of the nucellus. However, it is not uncommon for tubes to penetrate the nucellus

nearer its margins, in some cases reaching close to the edge of the nucellus (fig. 27). During the elongation of the tube there is also considerable increase in diameter, such that by the time the tube has reached the female gametophyte region its diameter is several times greater than at first (fig. 22). A striking enlargement now takes place. If the female gametophyte still consists of free nuclei, as it frequently does at this time, it may be so crowded upon by the enlarging tube as to be pushed to one side; or the megaspore membrane may remain quite firm, retaining its shape, the tube then being forced to conform its shape to that of the resisting megaspore membrane (fig. 28). A number of cases of branching tubes were found, the nuclear contents in such cases being near the point of branching, while the branches generally have dense cytoplasmic contents, indicating their haustorial activity. The enlarging tube usually spreads itself over the micropylar end of the female gametophyte; it may go off to one side and penetrate far into the nucellus; or it may grow along the side of the endosperm, passing by the archegonia in the micropylar end of the endosperm. If two female gametophytes are formed in an axial row, the pollen tube usually enlarges between them, while in some cases the pollen tube may entirely pass the developing female gametophyte and enlarge below it. It seems that in such cases the female gametophyte is developing from an upper megaspore (fig. 31).

In case the nucellus is invaded by a number of tubes they produce a rather interesting situation. The female gametophyte is crowded upon from several sides and is frequently pressed quite out of its normal shape. A case was found of an ovule which has no fewer than 22 pollen tubes, as indicated by their nuclear contents (fig. 32). The pollen tubes have completely invested the endosperm, considerably distorting it, and possibly preventing its normal development, although young archegonia are recognizable in it. In another case at least 9 tubes had enlarged about the endosperm, practically surrounding it, but in this case 3 of the archegonia had been fertilized and proembryos formed within them.

Apparently the tubes do not fuse even when in contact with one another, although when there are a number of tubes in an ovule

their enlargement and crowding upon one another produces such a complex that it is practically impossible to count the tubes except by their nuclear contents. The tubes which are on the periphery of the complex may be so crowded by the more interior ones as to remain quite narrow and their contained body cells may even be flattened by the pressure.

The cytoplasmic contents of the tube become quite vacuolated early in the growth of the tube and in early stages contain a large number of starch grains, although these apparently disappear in the later stages. The cytoplasm is always more abundant near the growing end of the tube, but when the tube enlarges at the forward end the bulk of the cytoplasm remains more or less closely connected with the nuclei of the male gametophyte. Frequently in late stages the cytoplasm may contain accumulated masses, irregular in shape and densely staining, and these may even be discharged into the egg cytoplasm at the time of fertilization.

DEVELOPMENT OF MALE GAMETOPHYTE.—Soon after pollination the microspore begins to elongate, and the first division into tube and generative cells takes place within 10–12 days after pollination (fig. 16). This division results in two unequal cells (fig. 17), the smaller generative cell being held in the base of the grain by a plasma membrane, while the larger tube cell forms the elongating tube. The division of nuclear material is no doubt equal, but the tube cell nucleus soon becomes larger than the nucleus of the generative cell, the former becoming ellipsoid and retaining this shape throughout the remainder of its history. The cytoplasm of the generative cell is denser than that of the tube cell.

As the tube elongates, the tube cell nucleus passes into the growing end, migrating rapidly behind the tip of the tube (figs. 19, 20). Even before the generative cell divides, the tube cell nucleus has usually gone some distance into the tube. The generative cell enlarges, pushes out its limiting membrane, and then divides. No case was found showing the second division, but that the two nuclei found together in the basal part of the tube (fig. 20) arose from the division of the generative cell can hardly be doubted. The basal one, the stalk cell, has a more vacuolated cytoplasm than that of the anterior body cell.

The body cell soon migrates into the tube and is followed by the stalk cell nucleus, the two usually being in contact and apparently having passed into the tube together. During the growth of the tube through the nucellus, up to the time when the pollen tube reaches the female gametophyte, the 3 nuclei are in an axial row, while later the stalk nucleus migrates around the body cell and takes a position besides the tube nucleus. Of these two nuclei in the tube, the tube nucleus is generally to be recognized by its being slightly larger than the stalk nucleus. The body cell begins enlarging at once after entering the tube. As it passes down the tube it is slightly ellipsoid, but on reaching the end of the tube, as the latter is enlarging about the endosperm, it becomes rounded as it increases in size. The cytoplasm remains dense and the nucleus becomes large. During the early history of the body cell its cytoplasm is uniformly distributed through the cell, but as it reaches its mature size the cytoplasm becomes less dense along the periphery and here shows delicate radial strands (fig. 23). The nucleus, which earlier occupied a central position, takes a more peripheral one (usually on the side opposite to that on which the stalk and tube nuclei lie), while the cytoplasm becomes considerably vacuolated along the margin of the cell, the radial strands disappearing with the increased vacuolization.

The division of the body cell into the two male cells takes place shortly before fertilization. Several mitotic figures of this division were found. The nucleus of the body cell being at one side of the cell, there is an unequal division of the cytoplasmic material. A broad spindle is formed and the cell plate laid down on it is lenticular in outline, resulting in the formation of the two unequal male cells, a small lens-shaped cell and a larger more rounded one. The nucleus of the larger cell takes a central position and enlarges, while with the growth of the nucleus of the smaller cell the latter soon has the appearance of a naked nucleus invested only by the nuclear membrane, the two cells remaining in contact with one another and being held together by the plasma membrane of the parent body cell (figs. 23–26). What is probably a similar situation in *Taxus baccata* has given rise to differences in the accounts as given by different workers. BELAJEFF (3) could not find a plasma

investment of the smaller nucleus. He speaks of "male nuclei" and not of male cells. His figure shows two nuclei in a common cytoplasmic mass. STRASBURGER (4) and JÄGER (6) both recognized two "cells." Miss ROBERTSON (18) figures the division of the body cell, but no cell plate is shown on the spindle, even in the late telophase; while her figure of the completed division lacks clearness on this point, owing to a possible inaccuracy in drawing or in technique. In her discussion she speaks of a "functional male nucleus" and "inequality of the sperm nuclei."

By the time the two male cells are formed, the vacuolization along the margin of the larger cell has become quite pronounced (fig. 26), and this continues until finally the cytoplasm has practically all withdrawn from the plasma membrane and collected about the nucleus. In this condition the male gametophyte has reached its maturity and fertilization may now take place. Should male cells fail to function in fertilizing an egg, as is frequently the case where there are a number of tubes in an ovule, they remain in this condition for a time and then disintegrate. Male cells have been found in ovules in which the proembryo was considerably advanced.

Two unequal male cells are reported for *Torreya taxifolia* (14) and *Cephalotaxus Fortunei* (16), and the division of the body cell into male nuclei in *C. drupacea* (17). Miss ROBERTSON concludes that there are formed "a functional male nucleus" and a "smaller male nucleus" in *T. californica* (18). In an earlier account (11) she had stated that the body cell divided into two nuclei of equal size. There is evident among the Taxineae a tendency toward the elimination of male cells in the formation of the so-called "male nuclei" only. The inequality of these nuclei or cells is another advance. A mere cutting off of the smaller nucleus from the body cell would be another step; while the final one, not known to be reached by any of the gymnosperms, would be a body cell functioning as a male cell. In *Taxus* the male gametophyte at its maturity consists of the stalk and tube nuclei and the two male cells. This is interesting in comparison with the angiosperm situation, in which the generative cell in its division produces the two male cells directly, thus eliminating one more

division between the microspore and the cells functioning in fertilization.

Female gametophyte

MEGASPORES.—STRASBURGER (2) long ago pointed out that in *Taxus baccata* the megaspore mother cells are the end cells of a series arising from the hypodermal layer of the nucellus, and that they are clearly distinguished from the surrounding cells by their larger size and larger nuclei. The same situation seems to hold for *T. canadensis*. STRASBURGER (2) claimed several megaspore mother cells; JÄGER (6) agrees with him, but COKER (9) in his study of *T. baccata* states that there is no evidence that more than one megaspore is ever formed. He says "the mother cell is hard to distinguish. At the time of its first division it is long and narrow, resembling very closely the cells adjoining." As to the number of mother cells, STRASBURGER was probably right. In my preparations I have found no difficulty in recognizing the megaspore mother cells, nor does there seem to be any doubt that there may be a number of them in an ovule. Only one, or occasionally two, may function, but other megaspore mother cells may be present, by all the other tests of a mother cell. The mother cells are distinguished from the other cells of the nucellus, not only by their size and the size of their nuclei, but by their different staining reaction. The group of mother cells may be recognized in the autumn or winter (fig. 33). The occurrence of two linear tetrads of megaspores (fig. 38) is sufficient evidence that there have been at least two megaspore mother cells in the case figured.

STRASBURGER (12) and COKER (9) have given rather complete descriptions of megaspore formation in *Taxus baccata*, and the process is essentially the same in *T. canadensis*, so far as my preparations show (figs. 34–38). In *T. baccata* the second division is said to be simultaneous in both daughter cells. This is probably the case in *T. canadensis* in most instances, although one case was found in which the division of the upper cell was completed before that of the lower (fig. 36).

Starch is present in considerable abundance in the megaspore mother cells as well as in the neighboring cells, and it is also found in the megaspores and in the developing female gametophyte.

STRASBURGER (12) states that the starch soon disappears from the megaspore mother cells of *T. baccata*, but COKER (9) in his figures shows starch grains in the megaspores as well as in the megaspore mother cells. The starch is not confined to the megaspore region, but is found abundantly in the adjoining cells, and some of it occurs throughout a considerable portion of the nucellus in *T. canadensis*.

The method of formation of a tapetum about the megaspore mother cells, as pointed out by STRASBURGER (12) in *T. baccata*, also holds for *T. canadensis*. These cells are formed more or less obliquely to the long axis of the megaspore cells (fig. 34), are rich in content, and stain differently from the megaspore mother cells. THOMSON (15) speaks of the tapetum derived from the nucellus as a "secondary tapetum," in distinction from forms in which the tapetum is derived from the sporogenous tissue, in which case it is called a "primary tapetum." GOEBEL pointed out long ago, however, that the significance of the "tapetum" is physiological, and not morphological, and that it may have a variety of origins. The megaspore mother cell seems to be the usual winter condition. While STRASBURGER (12) says the megaspore mother cells of *T. baccata* are completed in October and that further development takes place the next spring, this does not always hold for *T. canadensis*, as I have found young female gametophytes of several free nuclei in some of the material collected in November, 1913. Most of the ovules taken at this time showed the mother cell condition, but even in some of the ovules collected as late as December it may be doubted whether the megaspore mother cells had become fully matured. Evidently, therefore, the time for the maturity of the megaspore mother cells and the formation of megaspores may vary, yet the general statement may be made that the mother cell is the usual winter condition and that megaspore formation generally takes place in the spring with the renewal of the growing season.

Usually the innermost one of the linear tetrad of megaspores is the functional one, the 3 outermost then disorganizing and disappearing sooner or later (fig. 39). Any of the megaspores may function, however, as 1, 2, 3, or even all 4 of the megaspores may grow after their formation and more than one may divide in

the formation of young female gametophytes (figs. 39–44). The further development of several megaspores will be described later. Some interesting cases were found, such as those in which one of the upper megaspores had evidently functioned, while the lower ones had failed to develop, although still recognizable (figs. 30, 31). In both cases figured the pollen tubes have pushed past the gametophytes and penetrated to the central region of the nucellus.

THOMSON (**15**) in his investigation covering the megaspore membrane situation in the gymnosperms reports that in *Taxus canadensis* the megaspore membrane, while recognizable in the early free nuclear stages of the gametophyte, is practically unrecognizable in later stages. This agrees with my observations that the membrane is quite firm about the young female gametophyte, but seemingly fails to develop with the endosperm and is soon lost sight of. THOMSON associates this with the absence of the "primary tapetum" and regards it as a specialized advanced character, indicating that the Taxineae are "recent" as compared with some other forms.

DEVELOPMENT OF FEMALE GAMETOPHYTE

Free nuclear stage.—The first division of the functional megaspores takes place soon after their formation, and other divisions, which are always simultaneous, follow in rapid succession (figs. 39, 45, 46). The embryo sac enlarges as the number of nuclei increases. At first the nuclei are scattered in the embryo sac, but as this increases in size it becomes vacuolated in the center, the cytoplasm with the nuclei then taking a peripheral position, this condition being attained when the 8 or 16-nucleate stage is reached (figs. 47, 48). As reported by JÄGER (**6**) for *Taxus baccata*, about 8 successive divisions occur, resulting in approximately 256 free nuclei before wall formation takes place. The vacuole in the embryo sac has kept pace with the growth of the sac and the nuclei occur in the narrow cytoplasmic layer along the periphery, the cytoplasm not being uniformly distributed, however, but showing distinct radiations connecting the nuclei when seen in a tangential view (fig. 49).

In the enlargement of the embryo sac, if a lower megaspore is functioning, the growth seems to be downward; if an upper megaspore is functioning, the growth is upward; if two gametophytes

are developing, one grows upward, the other downward (fig. 51). In the early stages the embryo sac is usually pear-shaped, the narrow portion marking the original position of the megaspores, while the expanded portion shows the region of growth (figs. 47, 51). The growth of the embryo sac and the enlargement of the endosperm after walls have been formed crowd upon the adjoining cells of the nucellus in such a way as to distort and flatten them, while no doubt some of the nucellar tissue is also digested by the growing gametophyte.

Wall formation and growth of endosperm.—The first formation of walls between the nuclei results in a single layer of cells surrounding the central cavity (fig. 50). The cells at this stage are rich in starch, the starch grains having also been present during the free nuclear stages. Centripetal growth of these cells then begins by the radial lengthening of their walls, the walls reaching the center and forming a completely closed tissue before further cell division takes place. Several cases were found showing this feature in various stages, but in no case had periclinal walls formed before the tissue was closed (fig. 51). Cells which in a single section appear to be internal are merely the inner ends of cells abutting the margin in other sections. At the very narrow upper end the cells are very closely crowded together.

JÄGER'S account (6) of the formation of the endosperm in *Taxus baccata* differs in a few details from this, in that he states that the cavity is filled with tissue by the inward growth of a series of cells formed by periclinal walls. His technique was such, however, that he could easily have been mistaken in his interpretation of the situation. The filling of the central cavity by growth and periclinal divisions seems to be the rule among gymnosperms, and is probably to be correlated with the size of the cavity at the time wall formation begins. The smallness of the cavity in *Taxus* may account for the method of tissue formation found here.

Following the complete filling of the central cavity with cell tissue, periclinal walls come in, giving rise to several layers of cells between the margin and the center. Anticlinal divisions also take place soon and the growth of the endosperm in all directions continues. Archegonia soon appear in the micropylar end of the tissue.

Growth of the endosperm goes on rapidly, the greater meristematic activity being in the central portion, especially in the basal region. In the early history of the endosperm the cells are uninucleate, but as the embryo develops they become multinucleate, while in the central portion of the endosperm, below the growing tip of the embryo, the cells become elongated, forming a conducting tract for the food from the basal region of the ovule to the growing embryo. This elongation ceases to show after the embryo reaches maturity. In the mature endosperm, with the exception of the extreme micropylar portion, an abundance of food material is stored, this being the food supply of the seedling in the early stages of its germination.

A comparison of the size of the endosperm at different times in its development may be of interest. In fig. 52 there are shown 3 outline drawings, to the same scale, showing the comparative size of the endosperm at the time of wall formation (as in fig. 51), at the time of fertilization, and at the maturity of the seed. It is readily seen that the greatest growth of the endosperm takes place after fertilization.

Archegonia.—The archegonium initial arises from the outermost layer of cells and is recognizable very shortly after periclinal walls come in. The initials appear a short distance behind the "point" of the endosperm, but always occur in the micropylar end if the gametophyte is one which has developed from an inner megaspore; in case of a gametophyte from an outer megaspore the archegonia will be on the side of the gametophyte toward the center of the ovule. The initials can be recognized by their slightly larger size and by the size of their nuclei (fig. 53). The surrounding cells form the archegonial jacket. The initial divides into the primary neck cell and the central cell (fig. 54). The primary neck cell divides into several neck cells, all in the tangential plane, serving merely as a covering for the central cell, a "neck" hardly being recognizable. These neck cells become flattened, and by the time of the maturity of the archegonia are mere plates, usually with degenerate nuclei and but little cytoplasm.

The central cell enlarges to the mature size, and since in the large number of archegonia examined there were no indications of a

ventral canal cell or nucleus, it may be regarded that this central cell is the functional egg. This agrees with *Torreya taxifolia* (**14**). In *Cephalotaxus Fortunei* (**15**) and *C. drupacea* (**16**) a ventral nucleus is formed, in the latter disorganizing before fertilization. This marks the final elimination of the row of canal cells, an elimination which has been such a persistent and gradual process from bryophytes through pteridophytes and gymnosperms.

In the earlier stages of the archegonium the central cell nucleus is near the upper end of the cell, but as the archegonium matures it takes a more central position (fig. 55), the cytoplasm being somewhat vacuolated and supplied with an abundance of food material, some of which stains quite darkly with the staining agents used.

The archegonial jacket is recognizable from the initial to the mature archegonium, but is not strikingly conspicuous as in some other forms, and less so in the mature condition than earlier. Usually there is a jacket about each archegonium, with several layers of cells between the archegonia, but it is not a rare thing to see two archegonia with only a single layer of jacket cells between them, and several cases were found in which two archegonia were surrounded by a common jacket, this latter condition being an approach to the archegonium complex found in some of the other groups of gymnosperms. Several archegonia are usually present in a gametophyte, 4–8 being the average number.

SUPERNUMERARY GAMETOPHYTES.—Mention has been made of the fact that more than one megaspore may function. HOFMEISTER (**1**) long ago pointed out the presence of more than one embryo sac in *Taxus baccata*, and JÄGER (**6**), STRASBURGER (**12**), and Miss ROBERTSON (**18**) have found the same situation. STRASBURGER states that usually one embryo sac develops; if more than one starts, one is usually suppressed; but several times he observed two equally strong embryo sacs with more or less free peripheral nuclei, the two embryo sacs usually lying beside one another, and one case of one above the other. COKER (**9**) and THOMSON (**15**) found more than one embryo sac in *T. canadensis*, the former stating that one of the two gametophytes is smaller than the other, and while both may bear archegonia, the archegonia in the upper gametophyte face the pollen tube which has pushed in between the

two gametophytes, only the archegonia of the lower gametophyte, however, being fertilized.

In my material I find two gametophytes quite common, usually in an axial row, although sometimes lying side by side (fig. 57). One is usually larger than the other, the upper generally being the smaller of the two, and both may produce archegonia, as pointed out by COKER. Usually when 2 gametophytes develop in an axial row the pollen tubes push in between them, and then the archegonia are directed toward the tubes; but this is not always the case, as sometimes there are 2 apparently equally vigorous gametophytes, one above the other, and both with good archegonia in their micropylar ends. The pollen tube has spread out above the upper gametophyte, while the lower one is not in contact with the tube at any point in the case shown in fig. 58.

Several instances of more than 2 gametophytes in an ovule were found. One case (fig. 59) shows 3 gametophytes with tissue, the pollen tube lying between the two uppermost. No archegonia were present in the upper one, but both of the lower ones have good archegonia, one of which has been fertilized and contains a proembryo. Other cases show 4 gametophytes, in one of which (fig. 60) 2 of the gametophytes have formed tissue, while the other 2 are in free nuclear condition, archegonia being present only in the lowest, which also contains a proembryo, the pollen tube in this case having pushed its way between the 4 gametophytes. In another case (fig. 61) the ovule contains 3 gametophytes with tissue and archegonia, while the fourth one consists of only a few free nuclei and, although lying between two vigorous gametophytes with tissue, retains its shape, evidently owing to the firmness of the megaspore membrane. One ovule was found containing 5 gametophytes, 3 with free nuclei and 2 with tissue (fig. 62), only the lowest of the 5 having developed an archegonium. In this case more than one megaspore mother cell must have functioned. With two tetrads of megaspores (fig. 38) a situation such as this, and even with more gametophytes, is not impossible.

The mechanics by which the developing gametophytes become separated by the enlarging tube might be an interesting problem,

to which it may be suggested that there is an elongation of the nucellus during the growth of the gametophytes, together with a digestion of that portion of the nucellus immediately adjacent to them. The megaspores were evidently in contact when formed, but by the enlargement of the pollen tube between the young gametophytes they become widely separated as the tube develops.

Fertilization

While the fertilized egg represents a new phase in the life history and the account of it might be more properly included with that of the embryogeny, it may not be out of place to give a brief account of it in this connection. Ovules containing proembryos were found in material collected May 21. Preparations showing fertilization were found from this time on to as late as the middle of June, showing that the time for fertilization is not constant and may have considerable range.

At the time of fertilization the neck of the archegonium becomes ruptured and the nuclear contents and part of the cytoplasmic contents of the tube are discharged into the egg. The egg nucleus has migrated to the basal portion of the egg; the male nucleus with its investing cytoplasm comes in contact with the egg nucleus; the cytoplasm of the male nucleus invests the two nuclei lying in contact and forms a dense sheath about them (fig. 56). With the fusion of the two nuclei the act of fertilization is complete. The behavior of the chromatin in fertilization could not be determined from my material. The cytoplasmic sheath about the two nuclei also occurs in *Torreya californica* (**11**), *T. taxifolia* (**14**), and *Cephalotaxus Fortunei* (**16**) among the Taxaceae, as well as in several other cases reported, namely, by COKER (**8**) in *Taxodium;* by LAND (**13**) in *Ephedra;* and by NICHOLS (**19**) in *Juniperus communis* var. *depressa.*

The smaller male cell and the stalk and tube nuclei, together with the densely staining mass of the tube cytoplasm, when present, usually remain in the upper portion of the egg, where they sooner or later disorganize, although they may persist for some time and be recognizable at somewhat late stages of the proembryo or even after the suspensors have begun to elongate.

Time relations

The time periods involved in the reproductive process are always of interest in the gymnosperms, as use is made of this feature in determining the primitive or modern character of a group, those having short periods being regarded as the more advanced in this respect. In my material the time from microspore formation to pollination was about 6.5 months; from pollination to fertilization may be as short as one month, although fertilization generally occurs after a longer interval, the time between pollination and fertilization having a considerable range, with an accompanying range in the time of the maturity of the seed. I have collected mature seeds from the first week of July until late in September in central Pennsylvania. BELAJEFF (**3**) shows a pollen tube of *Taxus baccata* with two nuclei collected April 10 and a figure of fertilization dated May 26. JÄGER (**6**), at Zurich, reports pollination at the beginning or middle of March and fertilization at the end of May or beginning of June. Miss ROBERTSON (**18**) reports the time for fertilization at Kew to be about the middle of June. STRASBURGER (**4**) speaks of fertilization taking place the first half of July and the embryo complete by the end of August. None of these accounts gives so short a time period as I have found for *T. canadensis*.

Summary

Microspore formation takes place in the autumn. There are no indications of prothallial cells. The pollen grain is uninucleate when shed.

The pollen tube penetrates the nucellus very rapidly and enlarges excessively about the female gametophyte.

Three divisions take place in the development of the male gametophyte. The body cell divides into two unequal male cells, the larger of which functions in fertilization.

Several megaspore mother cells are formed, of which only one usually functions, although two of them may form megaspores. The megaspore mother cell is the usual winter condition, but megaspores may be formed and the female gametophyte may consist of several free nuclei before winter.

Following the free nuclear stage of the female gametophyte, radical walls come in, closing the cavity before the appearance of periclinal walls.

The archegonia appear early in the endosperm. The central cell is the functional egg, no ventral canal cell or ventral nucleus being formed.

More than one female gametophyte in an ovule is common; as many as 5 were observed.

In fertilization the nuclear contents of the pollen tube are discharged into the egg. A cytoplasmic sheath is formed about the two fusing nuclei.

From pollination to fertilization may be as short as one month. Mature seeds have been collected 6 weeks later.

In general the gametophyte history agrees with that reported for *T. baccata*.

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EXPLANATION OF PLATES XI–XIV

All drawings were made with a camera lucida and the figures illustrating a series of processes are drawn to the same scale in order to show comparative sizes. The original drawings are here reduced one-half. The magnification of the figures is approximately as follows: figs. 1–21, 23–26, ×570; fig. 22, ×92; figs. 27–32, 57–62, ×57; figs. 33–51, 53–56, ×268.

PLATE XI

FIG. 1.—Group of megaspore mother cells.

FIG. 2.—Synapsis preceding reduction.

FIGS. 3–7.—Stages in reduction division.

FIG. 8.—Two microspores are formed; second division in formation of other two not yet completed.

FIG. 9.—Complete tetrad of 4 microspores.

FIGS. 10–12.—Tetrads of more than 4 microspores, fig. 12 showing 6 microspores.

FIG. 13.—Portion of a microsporangium, showing wall, tapetum, and several microspores in winter condition.

FIG. 14.—Mature microspore at time of shedding.

FIG. 15.—Pollen grain after pollination has taken place, beginning to elongate.

FIG. 16.—First division of microspore.

FIG. 17.—Smaller generative cell and larger tube cell resulting from first division of microspore.

FIG. 18.—Stage slightly more advanced than preceding figure; tube nucleus passing into tube and cytoplasm becoming vacuolated.

FIG. 19.—Somewhat older tube, showing generative cell in forward end of tube enlarging before division, and large number of starch grains in cytoplasm of tube.

FIG. 20.—Generative cell has divided into basal stalk cell and anterior body cell, which already shows denser cytoplasmic contents than stalk cell.

FIG. 21.—Passage of stalk and body cells into tube.

FIG. 22.—Portion of an ovule (reconstructed from several sections) showing female gametophyte in nucellar tissue and several pollen tubes which have penetrated nucellus to female gametophyte.

FIG. 23.—Body cell at time of maturity, with laterally placed nucleus and delicate cytoplasmic radiations along periphery, together with stalk cell nucleus and tube nucleus.

FIG. 24.—Division of body cell.

FIG. 25.—Late stage in division of body cell; lenticular cell plate is shown, as well as vacuolization along margin of cell.

FIG. 26.—Mature male gametophyte, consisting of two unequal male cells, stalk cell nucleus, and tube nucleus.

PLATE XII

FIG. 27.—Portion of an ovule in which a branching pollen tube has passed to one side of nucellus.

FIG. 28.—Portion of an ovule showing more usual relation of pollen tube to female gametophyte.

FIG. 29.—Portion of an ovule in which pollen tube has passed to one side of female gametophyte, penetrating nucellus nearly to base of female gametophyte.

FIG. 30.—Portion of an ovule in which female gametophyte has developed from an upper megaspore, pollen tube having pushed past gametophyte.

FIG. 31.—Two pollen tubes have pushed past female gametophyte and enlarged below it; non-functioning lower megaspore is recognizable.

FIG. 32.—An ovule which contained no less than 22 pollen tubes; the figure is a reconstruction of several sections and shows the complex about female gametophyte and nuclear contents of several tubes.

FIG. 33.—Group of several megaspore mother cells.

FIG. 34.—Synapsis preceding reduction division of megaspore mother cell; division showing method of formation of tapetum.

FIG. 35.—The 2 cells resulting from first division of one of the two megaspore mother cells.

FIG. 36.—Megaspore tetrad, division of two lowest as yet incomplete.

FIG. 37.—Linear tetrad of megaspores.

FIG. 38.—Two linear tetrads of megaspores.

FIG. 39.—Innermost megaspore dividing, 3 outer ones degenerating.

FIG. 40.—Two-celled female gametophyte from division of inner megaspore; second megaspore has enlarged.

FIG. 41.—Inner megaspore divided, other 3 showing no signs of disintegration.

PLATE XIII

FIG. 42.—Four megaspores have enlarged considerably and nucleus of one has divided.

FIG. 43.—Second of the 4 megaspores has divided; first has enlarged somewhat, the two innermost retaining their normal size and appearance.

FIG. 44.—Third and fourth megaspores have each divided twice, second megaspore has enlarged, while outer one is beginning to degenerate.

FIG. 45.—Second division of megaspore.

FIG. 46.—Third division of megaspore; note beginning of formation of pear-shaped embryo sac.

FIG. 47.—An 8-nucleate female gametophyte.

FIG. 48.—Group in which first and third megaspores are disintegrating, second has enlarged considerably, while the fourth has produced an 8-nucleate female gametophyte.

FIG. 49.—Tangential view of a few nuclei and connecting cytoplasmic strands in free nuclear condition of female gametophyte.

FIG. 50.—Female gametophyte showing single layer of cells following first wall formation.

FIG. 51.—Two female gametophytes in axial row; upper one in free nuclear condition, lower with tissue just completed, completely closing embryo sac cavity; no periclinal walls have appeared, cells showing in interior being merely portions of cells whose outer ends abut on margin.

FIG. 52.—Female gametophyte at 3 different stages, at time of complete closing of cavity (fig. 51), at time of fertilization, and at maturity of seed, drawn to same scale, to show comparative size at different stages.

PLATE XIV

FIG. 53.—Upper portion of a female gametophyte showing 2 archegonium initials.

FIG. 54.—Two archegonia, showing young central and primary neck cells.

FIG. 55.—Mature archegonium; nucleus has become centrally placed, cytoplasm shows more or less radiations from nucleus and contains considerable food material; nuclei of neck cells degenerating.

FIG. 56.—Fertilization: male nucleus and egg nucleus are in contact at base of egg, surrounded by cytoplasmic sheath; smaller male cell nucleus and tube and stalk cell nuclei can be seen in upper portion of egg cytoplasm; ellipsoid dark bodies are food particles, while irregular dark mass seen in upper portion of egg is an accumulated mass of cytoplasm from pollen tube.

FIG. 57.—Two female gametophytes lying side by side, with innermost portions of 2 pollen tubes beside them.

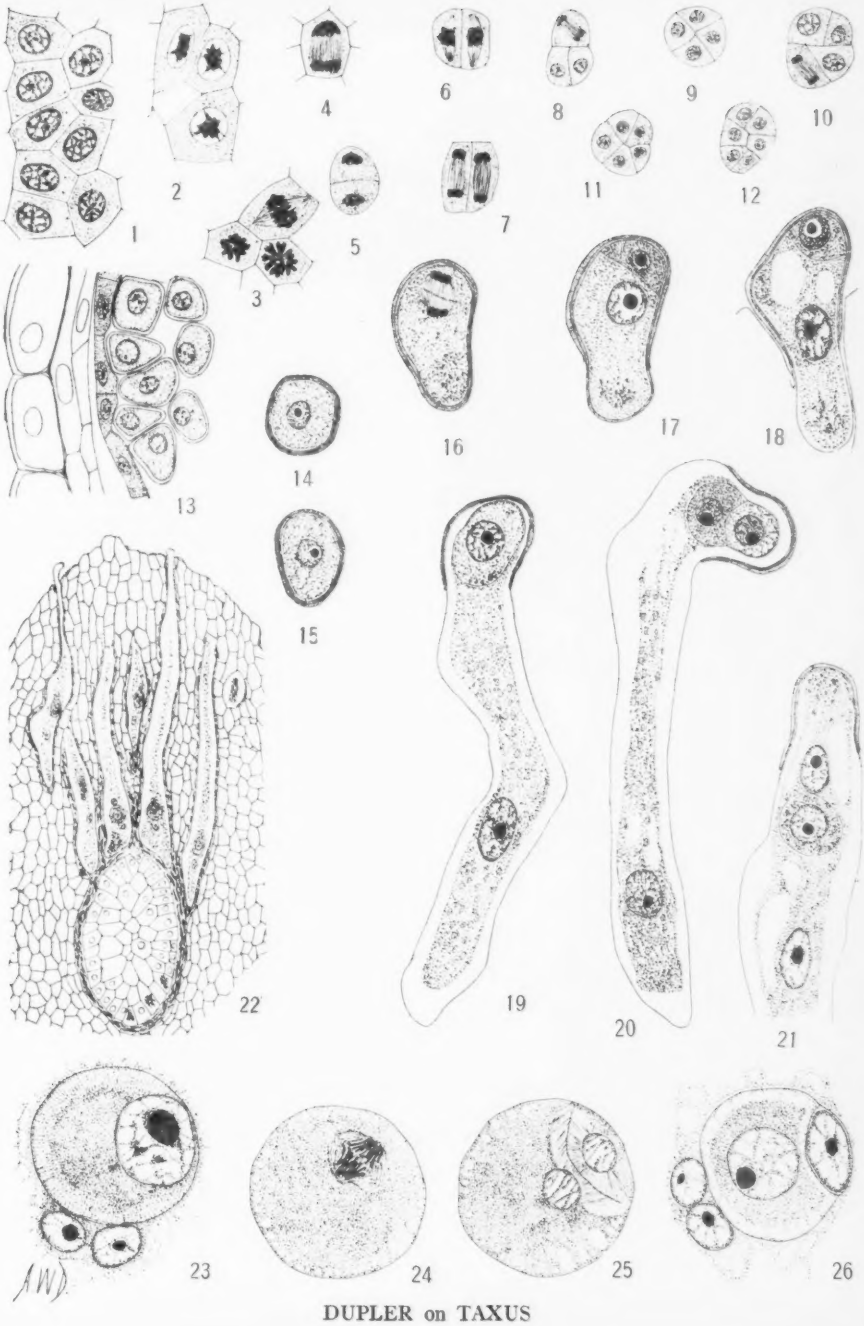
FIG. 58.—Two gametophytes in axial row, both having developed good archegonia; pollen tube has spread out over micropylar end of outer gametophyte.

FIG. 59.—Three female gametophytes in axial row, with pollen tube between first and second; second contains a proembryo, while inner one also contains a good archegonium.

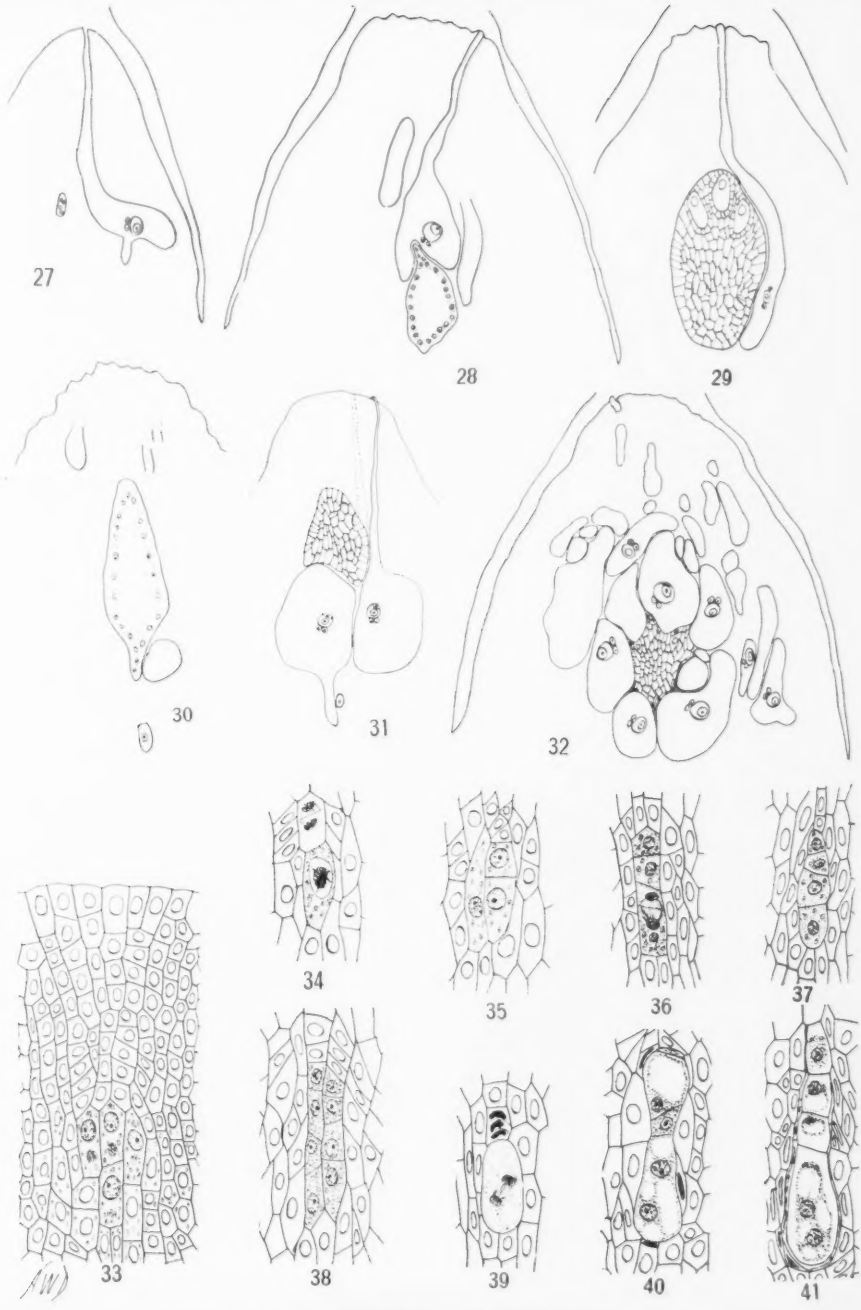
FIG. 60.—Ovule containing 4 female gametophytes, 2 of which are in free nuclear condition; lower one contains a proembryo; pollen tube has crowded between the 4 gametophytes.

FIG. 61.—Another ovule with 4 female gametophytes, 3 of which contain archegonia; one of gametophytes consists of only a few free nuclei, but has not been pressed out of shape by its neighbors; pollen tube is shown below upper gametophyte.

FIG. 62.—Portion of ovule with 5 female gametophytes, 3 of which are in free nuclear condition, and an archegonium appearing only in lower of two with tissue; enlarging pollen tube has widely separated 3 upper gametophytes from 2 lower ones.



DUPLER on TAXUS



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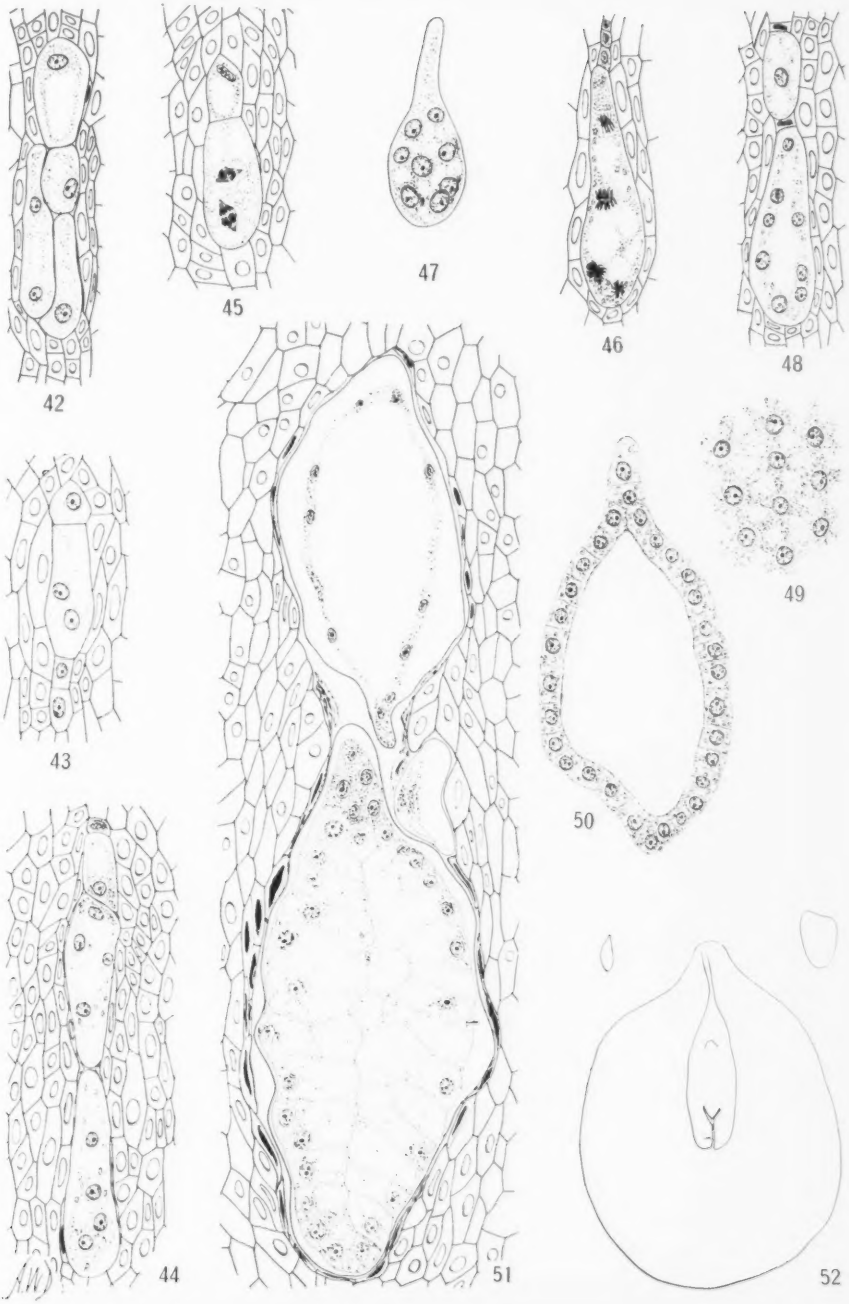

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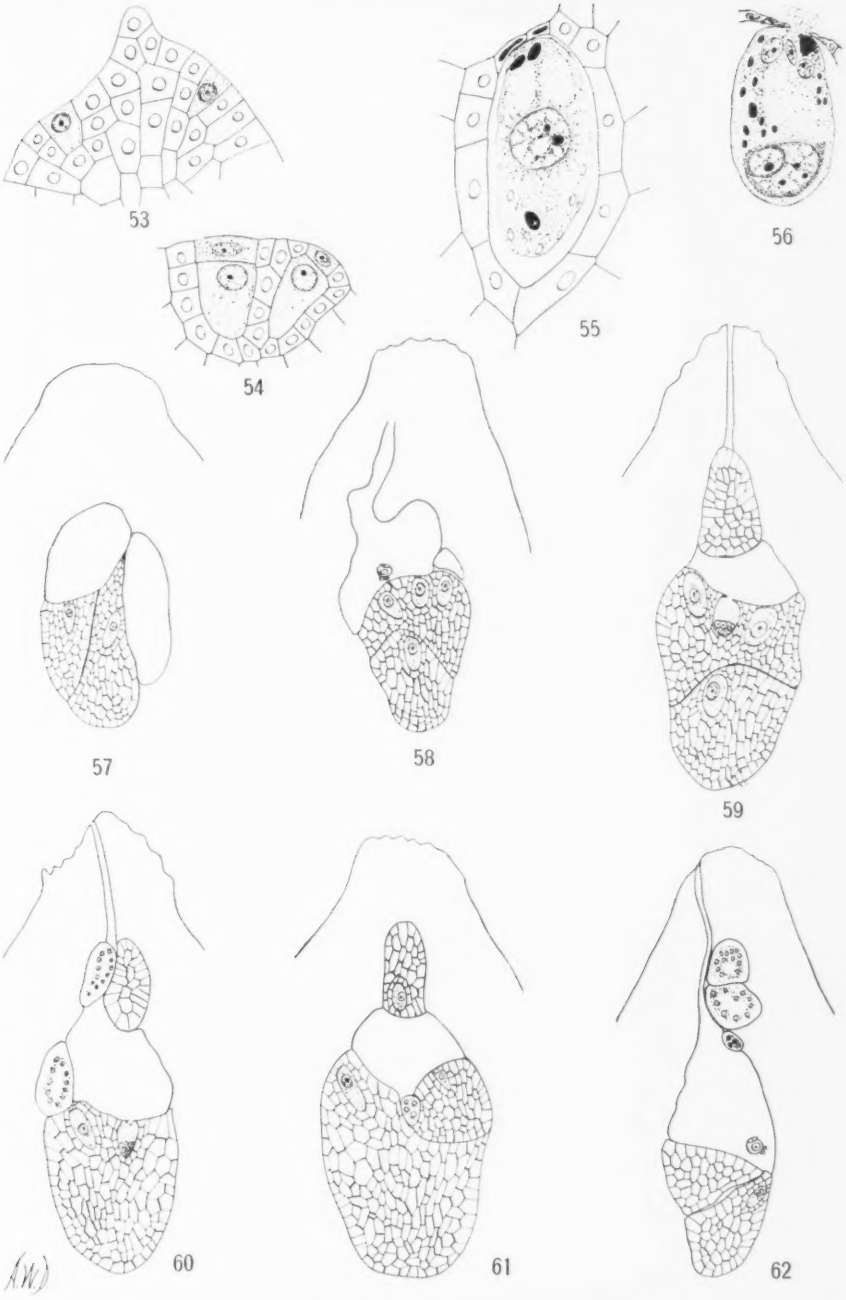


DUPLER on TAXUS

ARBORES FRUTICESQUE CHINENSES NOVI. IV

CAMILLO SCHNEIDER

(WITH PLATE XV)

Salix (sect. SCLEROPHYLLAE Schn.) **tenella,** n. sp. (fig. A, 1–6).—Frutex parvus squarrosus; ramuli hornotini non visi, annotini biennesque floriferi obscure purpurascentes, minute puberuli vel fere tomentelli, dein glabrescentes, vetustiores cinerascentes vel cinereo-brunnei. Folia nondum satis evoluta anguste elliptico-lanceolata, apice obtusa, basi subrotundata, 1–1.5 cm. longa, 0.2–0.4 cm. lata, superne viridia, initio plus minusve puberula, subtus discoloria, glaucescentia, sparse puberula vel ut videtur cito glabrescentia, nervis valde tenuibus utrinsecus circ. 6 superne incisis, margine integerrima; petioli 1–2 mm. longi, pilis subflavis tomentelli. Amenta tantum juvenilia feminea visa, coetanea, anguste cylindrica, 3–4 mm. crassa, ad 2.5 cm. longa, pedunculis folia 3–6 parva normalia gerentibus puberulis circ. 5 mm. longis exclusis, rhachi tomentella, densiflora; bracteae ovato-rotundae vel ovato-ellipticae, ovariis sublongiores, supra medium fuscae, apice subrotundatae, tantum versus basim laxe pilosae et paullo ciliatae, ceterum glabrae; ovaria sessilia, ovata, glabra vel partim sparse pilosa, stylo brevissimo ad basim bifido coronata; stigmata brevia, biloba; glandulae 2, ventralis late ovata vel ovato-rectangularis, dorsalis paullo minor, similis vel 2-partita.

Szechuan australis: in districtu Yen-yüan Hsien, prope pagum Liu-ku, ad vias, alt. circ. 3600 m., 18 Maji 1914, *C. Schneider* (no. 1304; typus in Herb. Arb. Arn. et Hb. Schneider; frutex parvus).

This species very much resembles some forms of sect. LONGIFLORAE Schn., but, according to the dorsal gland, it seems closely related to *S. atopantha* Schn., which may easily be distinguished by its hairy ovaries and bracts, and by the different shape of its ventral gland. The very young leaves of *S. tenella* show no distinct sign of a dentation.

Salix (sect. ERIOSTACHYAE Schn.) **Balfouriana,** n. sp. (fig. B, 1–4).—Arbuscula erecta, pulchra, ad 6 m. alta; ramuli annotini

subdense albo-villosuli, deinde fuscescentes vel nigrescentes, glabrescentes vel subglabri; gemmae juveniles dense villosae. Folia satis magna, late elliptica vel elliptico-oblonga, apice subito breviter acuta, basi rotundata, rarius leviter subcordata, minora inferiora 6–8 cm. longa, 2–3 cm. lata, majora superiora 9–12 cm. longa et 3.3–4.8 cm. lata, superne saturate viridia, adulta laxe (in costa densius) sericeo-villosula, subtus valde discoloria, pulcherrime albescentia, pruinosa (non papillosa), plus minusve (initio probabiliter dense) adpresse albo-sericeo-villosula, costa nervisque lateralibus utrinsecus circ. 8–12 angulo 50–80° a costa divergentibus flavescentibus utroque latere prominentibus, reticulo nervillorum gracillimo prominulo, margine integerrima; petioli 6–15 mm. longi, undique dense villosi, superne late sulcati; stipulae ut videtur minimae, indistinctae. Amenta tantum fructifera visa, tardiva, ramulos foliatos 1.5–4 cm. longos terminantia, cylindrica, ad 8 cm. longa et 1 cm. crassa, axi dense villosula. Flores adulti inter fructus remanentes circ. 6 mm. longi; ovaria ovato-oblonga, sessilia, dense albo-villosula; styli distincti circ. $\frac{1}{4}$ ovarii aequantes, ad basim bifidi, stigmatibus satis marcidis angustis oblongis bifidis brachiis styli fere aequilongis; glandula 1, ventralis, sicca ovato-trangularis, brevis; bracteae late ellipticae, apice rotundatae, pallidae vel brunnescentes utrinque villosae, ovario subtriplo breviores. Fructus maturi circ. 7 mm. longi, ovariis adultis similes, aperti valvis paullo recurvis.

Yunnan boreali-occidentalis: ad latera orientalia montium niveorum prope Lichiang-fu, in dumetis in valle magna infra glaciem magnam, alt. circ. 3400 m., 30 Julii 1914, *C. Schneider* (no. 2059; typus in Herb. Arb. Arn. et Hb. Schneider; arbuscula ad 6-metralis).

Unfortunately I collected only a few remnants of fruiting catkins, and I have seen neither young female flowers nor the male plant, but the leaves are so distinct that there can be no doubt that this willow represents an excellent new species. So far as I can judge by the material before me, it belongs to sect. ERIOSTACHYAE Schn., but it may be distinguished at once from all the other species by the beautiful snowy white under surface of its leaves.

To this species may also belong a sterile specimen collected by me in Szechuan australi, inter Hoh-si et Te-li-pu, alt. circ. 2000 m., 7 Maji 1914 (no. 1124; arbor parva ad 5-metralis). It differs from the type in having somewhat narrower ovate-oblong leaves which are much more acute at the apex, the larger ones measuring up to 9 cm. in length and up to 3 cm. in width.

The name is given in honor of Professor BAYLEY BALFOUR, the distinguished Scotch botanist and director of the Royal Botanic Garden at Edinburgh, which contains an extremely rich collection of living woody and herbaceous plants from China, especially from northwestern Yunnan.

Salix (sect. PSILOSTIGMATAE Schn.) **Guebriantiana,** n. sp. (fig. C, 1–5).—Frutex erectus, satis elongato-ramosus, ad 6 m. altus; ramuli novelli initio parce sericei, annotini biennesque glabri, rubro-fusci vel sordide brunnei; gemmae flavo-rubrae, oblongae, subglabrae. Folia juvenilia ovato-oblonga vel late lanceolata, apice sensim subacuminata, basi cuneata vel rotundata, 3–5 cm. longa et 1–1.5 cm. lata, superne initio sericea vel sericeo-villosa, cito subglabra, intense viridia, subtus plus minusve dense sericeo-villosa, dein glabrescentia, discoloria, pruinosa, nervis lateralibus utrinsecus circ. 12 angulo acuto a costa divergentibus, margine integerrima vel saepissime versus apicem dense minute glanduloso-serrata, matura ignota; petioli vix 5 mm. longi, laxe sericei; stipulae distinctae non visae. Amenta (mascula tantum visa) coetanea, anguste cylindrica, nondum satis evoluta ad 6.5 cm. longa et vix 7 mm. crassa, pedunculo ad 1 cm. longo folia 3–4 normalibus minora sed similia gerente excluso, axi laxe villosa; bracteae concolores pallidae vel apice leviter brunnescentes, obovato-orbiculariae, apice plus minusve truncatae et saepe leviter crenulatae, basi dorso leviter saccatae, glabrae, filamentis subduplo vel fere 3plo breviores, quam glandula dorsalis subduplo longiores; filamenta glabra, juvenilia satis crassa; antherae flavae, ovato-globosae; glandulae 2, separatae, ventralis lata, subquadrato-rotundata vel rectangularis et apice truncata, dorsalis illae vix vel paullo brevior sed angustior, oblonga, apice truncata.

Szechuan australis: inter urbem Yen-yüan Hsien et viculum Hun-ka, in dumetis collinis, 11 Junii 1914, *C. Schneider* (no. 1488; typus in Herb. Arb. Arn. et Hb. Schneider; frutex erectus vel arbuscula ad 6-metralis).

In its long narrow catkins this species very much resembles *S. phanera* Schn. and its relatives, but it may be distinguished from them at once by its glabrous bracts and filaments, as well as by the different shape of its broad ventral gland. The male flowers are not unlike those of *S. magnifica* Hemsl., which otherwise is extremely different. Unfortunately there are neither mature leaves nor female flowers, and without having seen those the relationship of this well marked species remains doubtful.

I take great pleasure in associating with this interesting willow the name of Mgr. DE GUÉBRIANT, bishop of the famous French Catholic Mission at Ning-yüan-fu, in appreciation of valued service rendered to me while I was staying in that town during the month of April 1914.

Salix (sect. PSILOSTIGMATAE Schn.) **wolohoensis,** n. sp. (fig. D, 1–5).—Frutex erectus, squarrosus, ad 2 m. altus; ramuli, novelli tomentosuli, dein glabrescentes, olivaceo-brunnescentes, biennes glabri, fuscescentes; gemmae foliiferae ovatae, obtusae, adpressae, breviter pilosae, flavobrunneae, circ. 4 mm. longae. Folia firma, etiam majora vix satis evoluta, late lanceolata vel anguste elliptico-lanceolata, apice sensim acuta vel minora subobtusa, basi late cuneata vel rotundata, minimis exceptis inferiora 3–4 cm. longa et 1–1.5 cm. lata, superiora ad 7 cm. longa et 2 cm. lata, superne sordide viridia, initio densius dein laxe adpresse sericeo-villosa, costa flavescente plana, nervis lateralibus subincisis, subtus valde discoloria, initio tomento sericeo subflavescente dense tecta, dein argenteo-cinerea, adpresse sericeo-villosa (pilis costae parallelibus), costa nervisque lateralibus circ. 8–10 angulo 45–60° a costa divergentibus flavescentibus prominulis, rete nervillorum haud vel indistincte prominulo, margine integerrima vel obscure minutissime distanter glanduloso-denticulata; petioli 2–4 mm. longi, superne sulcati, tomentosuli; stipulae minimae 2–3.5 mm. longae, semicordatae, glanduloso-denticulatae, ut folia pilosae. Amenta tantum fructifera visa, subsessilia, pleraque delapsa, ad 4 cm. longa et ad 8 mm. crassa, patentia, ad axim villosula, basi foliolis paucis parvis vix ad 1 cm. longis deciduis ceterum normalibus satis similibus instructa; flores inter fructus remanentes circ. 3 mm. longi; ovaria ovata, dense sericeo-villosula, sessilia; styli breves integri, stigmatibus iis aequilongis oblongis bifidis; glandula 1, ventralis, ovario 3-plo brevior, oblongo-rectangularis, apice truncata vel retusa (an juvenilis longior?); bracteae late obovato-orbiculares, apice subretusae, ovario subduplo breviores, distincte brunnescentes, intus subglabrae, extus laxe sericeo-villosae, margine praecipue apice pilis albis sericeis satis brevibus fere comoso-ciliatae. Fructus circ. 5 mm. longi, ovati, satis obtusi, aperti valvis strictis, bracteis quam in flore glabrioribus brevioribus, ceterum ut ovaria superne descripta.

Szechuan australis: inter oppida Yen-yüan Hsien et Yung-ning, in dumetis inter pagos Wo-lo-ho et Hu-ma-ti, alt. circ. 2000–2400 m., 16 Junii, *C. Schneider* (no. 3490; typus in Herb. Arb. Arn. et Hb. Schneider; frutex squarrosus ad 2-metralis).

This species much resembles *S. psilostigma* And., which I only know from the good specimens collected by A. HENRY and G. FORREST in Yunnan and mentioned by me in the Pl. Wils. 3: 116. From those the new species may be distinguished by its leaves being a little more hairy on the upper surface and not so thickly covered with a silvery silky pubescence on the lower one, by its much more glabrous bracts which are not densely silky outwardly, and by its shorter, entire, not deeply cleft styles. The fruiting catkins seem to be shorter in *S. wolohensis*. Without having seen the male plant, it seems impossible to determine the real relationship of this species, which comes from a region that has never been explored before by botanical collectors.

Salix (probabiliter sect. DENTICULATAE Schn.) **caloneura,** n. sp. (fig. G, 1–6).—Frutex elatior, divaricatus; ramuli hornotini annotinique glabri, flavescentes vel olivacei, vetustiores rubro-brunnei, interdum ad gemmas adpressas puberuli. Folia elliptica, obovato-elliptica vel maxima late elliptico-oblonga, apice satis subito breviter acuta, basi obtusa vel subrotundata, interdum subcuneata, superne intense viridia, subtus valde discoloria, albescentia, sub microscopio plus minusve papillosa, costa nervisque flavescentibus utrinque prominulis, nervis lateralibus versus marginem currentibus approximatis circ. 3–4 pro 1 cm. conspicuis, rete nervillorum satis distincto, valde juvenilia subtus distincte sericea, mox glabrescentia, adultiora superne ad costam sparse vel vix puberula, subtus in costa pilis sparsis praedita vel glabra, margine integerrima vel saepissime indistincte crenulata, ima basi interdum glandulis indistinctis 2 instructa, minora inferiora 4–7 cm. longa, 2–3.5 cm. lata, maxima superiora ad 9:3.5 vel 10:3 cm. magna; petioli 0.5–1.5 cm. longi, superne in sulco pubescentes. Amenta tantum fructifera visa, densa, ad 7 cm. longa et 1 cm. crassa, axi glabrescente, pedunculo ad 1.5 cm. longo folia satis parva sed normalia 3–4 gerente suffulta. Flores feminei inter fructus remanentes glaberrimi; ovaria ovato-oblonga, pedicellis glandulam unam ventralem anguste rectangularem apice truncatam fere duplo vel vix superantibus, stylo satis distincto fere ad basim bifido stigmatibus parvis brevibus satis obtusis longiore; bracteae ut videtur ovato-ellipticae, glabrae, fuscescentes, pedicellum ovarii circ. $\frac{1}{3}$

superantes. Fructus maturi circ. 6 mm. longi, ovato-elliptici, glabri, ut ovaria pedicellati, pedicello glandulam siccam fere duplo superante.

Szechuan australis: in districtu Hua-li ad flum. Yalung, in dumetis, alt. circ. 2800 m., 27 Maji 1914, *C. Schneider* (no. 1425; typus in Herb. Arn. Arb. et Hb. Schneider).

Judging by the fruiting material only, I believe this species is best placed in sect. DENTICULATAE Schn. near *S. denticulata* And., but it can be distinguished at once from this species by its much larger leaves. The yellowish nervation is very conspicuous on both surfaces of the leaves. I am not able to determine the real relationship of the new species, not having seen any male specimen.

Salix (probabiliter sect. PHYLICIFOLIAE Dum.) **squarrosa,** n. sp. (fig. E, 1–5).—Frutex erectus, squarrosus, breviter ramosus, ad 4 m. altus; ramuli hornotini non visi, annotini nigro-purpurascentes, glabri vel praesertim ad gemmas parce pilosiusculi, biennes sordide brunnescentes vel ut vetustiores nigro-cinerascentes; gemmae foliiferae elliptico-oblongae, acutae, subadpressae, circ. 1 cm. longae, flavo-brunneae, glabrae. Folia nondum evoluta vel minima, vix ad 1 cm. longa et 3 mm. lata, superne glabra, subtus dense longe sericea sed ut videtur cito glabrescentia, integerrima, nervis lateralibus vix visibilibus, matura ignota. Amenta praecocia, sessilia, patentia, ovato-elliptica, vel breviter cylindrica, 1.5–2.8 cm. longa, circ. 1 cm. crassa, dense albo-sericea, tantum feminea visa; bracteae ovatae, subacutae, ovaria florum superantes sed vix apicem styli attingentes, nigro-fuscae, utrinque longe sericeae; ovaria ovata, dense breviter sericea, breviter pedicellata, pedicello glandulam aequante vel sublongiore; styli fere glabri, distincti, elongati, dimidio ovarii aequilongi, stigmatibus oblongis apice haud vel paullo emarginatis stylo brevioribus coronati; glandula una, ventralis, oblongo-rectangularis, apice truncata. Fructus vix satis maturi pedicello stigmateque incluso circ. 6 mm. longi, ovato-elliptici, ut ovaria sericei, bracteas subduplo superantes.

Szechuan australis: in districtu Yen-yüan Hsien, inter viculos Ka-la-pa et Liu-ku, in silvis montanis, alt. circ. 3800 m., 16 Maji 1914, *C. Schneider* (no. 1246; typus in Herb. Arb. Arn. et Hb. Schneider; frutex squarrosus, circ. 4 m. altus).

This is the first willow from central China, I have seen, which apparently represents a species of sect. PHYLICIFOLIAE Dum. It is a much branched tall shrub with short spreading branchlets. The short, silky female aments are perfectly sessile. Without having seen mature leaves and male flowers, however, it is impossible to be sure of the real relationship of the species.

Salix (sect. DIPLODICTYAE Schn.) **Faxoniana,** n. sp. (fig. H, 1–5).—Frutex parvus, ramis prostratis radicantibus, ramulis ascendentibus, 0.2–0.3 m. altus; ramuli tantum novelli initio sericei, annotini glabri, flavo-brunnei, biennes vetustioresque obscure brunnescentes, deinde nigrescentes; gemmae elliptico-oblongae, subacutae, circ. 5 mm. longae, glabrae. Folia obovato-elliptica, elliptica vel elliptico-oblonga (vel minima ovato-elliptica), apice rotundata, obtusa vel breviter subacuta, basi late cuneata vel rotundata, 1.5:1 cm. ad 3.5:2–2.3 cm. vel angustiora ad 3:1.5 cm. magna, superne intense viridia, subnitidula, glabra, tantum in costa subimpressa vel plana versus basim pilis sparsis praedita, subtus valde discoloria, cinerascentia vel albescentia, pruinosa, in costa nervisque lateralibus prominulis utrinsecus 6–10 angulo 70–80° a costa divergentibus pilis sericeis sparsis instructa vel glabra (juvenilia probabiliter dense sericea), reticulo nervillorum satis distincto, margine satis indistincte et distanter glanduloso-crenato-denticulata; petioli satis longi, superne in sulco lato plus minusve puberuli, 8–13 mm. longi. Amenta tantum fructifera visa, ramulos ad 3 cm. longos normaliter foliatos terminantia, cylindrica, densiflora, ad 5 cm. longa et circ. 1 cm. crassa, axi laxe villosula; bracteae florum inter fructus remanentium oblongae, fuscae, obtusiusculae, dimidio ovarii aequantes, versus basim parce villosulae, apicem versus glabrae, plus minusve ciliatae; ovaria elongata, conica, basi in pedicellum brevissimum quam glandula duplo breviorem attenuata, glabra vel basi sparse villosula; styli distincti, ovariis junioribus $\frac{1}{3}$ vel subduplo breviores, fere ad medium fissi, brachiis divaricatis stigmatibus parvis brevibus bifidis coronatis; glandula una ventralis, oblonga, obtusa, pedicellum duplo superans. Fructus circ. 8 mm. longi, apice attenuati, aperti valvis recurvatis, glabri vel ima basi puberuli, bracteis et glandulis siccis ut in ovario minoribus.

Yunnan boreali-occidentalis: in rupestribus ad latera orientalia montium niveorum prope Lichiang-fu, alt. circ. 4000 m., mense Augusto 1914, C.

Schneider (no. 2319; typus in Herb. Arb. Arn. et Hb. Schneider; frutex 0.2–0.3 m. altus); in declivibus rupestribus montium inter flum. Yang-tze et oppidum Chung-tien, alt. circ. 3400 m., mense Augusto 1914, *C. Schneider* (no. 2375; forma nullo modo ab no. 2319 diversa).

At first sight this species very closely resembles *S. oreinoma* Schn. from the high mountains of western Szechuan, but *S. Faxoniana* differs from it and from the other Asiatic species of sect. DIPLODICTYAE Schn. in its glabrous ovaries, the fruits being sometimes hairy only at the very base. The leaves are similar to those of *S. oreinoma*, but the catkins of this species measure only about 2 cm. in length (without the peduncle), and the bracts are more glabrous, broader, and truncate at the apex. The species is named in compliment to MR. C. E. FAXON, the assistant director of the Arnold Arboretum.

SALIX BRACHISTA Schneider in Sargent, Pl. Wils. **3**:145. 1916.—I described only a male specimen, and I add the following description of the female plant: Frutex pygmaeus, trunco subterraneo, ramis procumbentibus radicantibus; ramuli prostrati, initio olivacei vel flavescentes, dein flavo-brunnei vel flavo-rubri, tantum novelli parce pilosuli, cito glabrescentes. Folia parva vel perparva, crasse papyracea, elliptica vel ovato-elliptica, utrinque acuta vel pleraque apice acutiuscula et basi subrotundata, minimis exceptis 6:2 mm. ad 12:6 mm. vel maxima ad 17:9 mm. magna, superne satis viridia, costa incisa, nervis lateralibus planis vel vix levissime prominulis, glabra, subtus pallidiora, non glaucescentia, costa nervisque lateralibus utrinque 5–7 angulo circ. 50–70° a costa divergentibus distincte prominulis, an initio pilosa?, adulta glabra, margine subintegerrima vel plus minusve distanter minute denticulata; petioli glabri, superne sulcati, 2–4 vel foliorum maximorum ad 8 mm. longi, gemmas plus minusve duplo superantes. Amenta fructifera pauca tantum visa, ramulos breves normaliter paucifoliatos terminantia, 2–4-flora; fructus maturi, obovato-oblongi, apice attenuati, 6–7 mm. longi, glabri, brunnei, aperti valvibus apice recurvatis, subsessiles, pedicello glandula subbreviore; styli sicci breves, stigmatibus ut videtur brevibus coronati; glandula 1, ventralis, satis late rectangularis, pedicello sublongior; bracteae pallidae, glabrae, obovato-oblongae, apice retusae vel rotundatae, capsulis fere duplo breviores.

Yunnan boreali-occidentalis: ad latera orientalia montium niveorum prope Lichiang-fu, in rupestribus calcareis in valle infra glaciem magnam, alt. circ.

3500 m., mense Augusto 1914, *C. Schneider* (no. 3454; ramuli fructiferi in Herb. Schneider).

It is with some hesitation that I refer this female willow to *S. brachista* Schn., which is known only from male specimens collected by E. H. WILSON in western Szechuan. In most of my specimens there are no flowers or fruits, the apex of the branchlets being infected probably by an insect and transformed into hairy galls. The leaves agree well with those of typical *S. brachista* in the nervation and color.

Together with no. 3454, I collected another female willow (no. 2318), the leaves of which are even a little smaller, of a somewhat firmer texture, with veins slightly impressed above and scarcely visible on the rather bluish grey under surface. I am not sure whether or not this form belongs to the Himalayan *S. Lindleyana* Wall. or represents a form of *S. Souliei* Seemen. It is not quite identical with those female plants from Tachien-lu which I described in Pl. Wils. **3**:62 as *S. Souliei*. I think it best, therefore, to give the following description of no. 2318 from the snow mountains near Lichiang-fu:

Frutex pygmaeus facie *S. Lindleyanae* Wall. vel *S. serpyllifoliae* Scop. ramis solo vel rupestribus adpressis, ramulis brevibus junioribus olivaceis glabris (an novellis pilosiusculis?). Folia perparva, crassiuscula, elliptica vel ovato-elliptica, utrinque obtusa vel subacuta, rarius basi subrotunda, minimis exceptis 5–7 mm. longa, 2–3 mm. lata, superne satis laete viridia, glabra vel in costa incisa sparse pilosa, nervis lateralibus plus minusve distincte incisis, subtus satis discoloria, glaucescentia (etiam novella?), costa prominula, nervis lateralibus utrinsecus 2–4 angulo 40–45° a costa divergentibus vix vel haud visibilibus, margine integerrima vel saepius plus minusve minute denticulata; petioli distincti, 2–4 mm. longi, superne interdum pilosiusculi, gemmas duplo superantes. Amenta ramulos perbreves normaliter foliatos terminantia, fructifera subcapitata, circ. 5-flora, in axi sparse pilosa; flores adulti glaberrimi, circ. 4–4, 5 mm. longi; ovaria ovato-conica, apice attenuata, basi plus minusve pedicellata, pedicello glandula sublongiore vel subbreviore; styli breves sed distincti, ad medium bifidi, stigmatibus brevibus oblongis emarginatis bifidisve brachiis styli subaequilongis; glandula 1, ventralis, oblongo-rectangularis, apice truncata; bracteae flavescentes vel in sicco flavo-brunneae obovato-oblongae vel oblongo-ellipticae, apice rotundatae, retusae vel emarginatae, ovariis circ. $\frac{1}{3}$ breviores. Fructus maturi ovati, aperti valvibus apice paullo recurvis, ceterum ut ovaria (fig. F, 1–4).

Salix (? sect. SIEBOLDIANAE Seem.) **dibapha,** n. sp. (fig. I, 1–6).—Frutex erectus, ad 4 m. altus, ramuli hornotini laxe vel densius villosuli (novelli satis dense flavescenti-tomentelli), annotini satis glabrescentes, atro-fusci, vetustiores glabri; gemmae foliiferae ut videtur flavo-purpureae, subglabrae. Folia papyracea, elliptica vel elliptico-oblonga, apice acuta vel longiora sensim breviter acuminata, basi cuneata, superne vivide laete viridia, tantum valde juvenilia plus minusve flavescenti-sericeo-tomentella, costa prominula nervisque partim exceptis cito glabra, subtus valde discoloria, glauca, pruinosa, initio ut supra sericeo-tomentella, sed citissime glabrescentia, tantum in costa elevata parce sericea, nervis lateralibus utrinsecus 10–20 angulo 80–90° a costa divergentibus prominulis, reticulo nervillorum foliorum immaturorum valde tenui vel vix visibili adultorum probabiliter magis conspicuo, margine integerrima, minimis exceptis inferiora elliptica 4–6 cm. longa et 1.4–2 cm. lata, superiora oblongiora ad 8:2.4 cm. magna; petioli 4–7 mm. longi, undique sericeo-villosuli; stipulae minimae, semicordato-lanceolatae, villosulae, margine glanduliferae, vix ad 3 mm. longae. Amenta tantum fructifera visa, praecocia, elongato-cylindracea, pedunculo ad 1 cm. longo foliola pauca parva ad 1.5 cm. longa ab normalibus vix diversa gerente excluso ad 8 cm. longa et 0.9 cm. crassa, axi villosa; flores inter fructus remanentes 2–3.5 mm. longi; ovaria ovata, sessilia, dense villosula; styli breves sed distincti, $\frac{1}{4}$–$\frac{1}{5}$ ovarii aequantes, apice breviter bifidi, stigmatibus brevibus subbifidis oblongis; glandula 1, ventralis, oblonga, satis brevis, bracteis florum adultiorum subduplo brevior; bracteae ovariis juvenilioribus aequilongae, elliptico-oblongae, obtusae, brunnescentes, intus glabrae, extus infra medium villosulae et ciliatae, apice glabrae, ovariis adultioribus fere 3-plo breviores. Fructus subsessiles, ovato-oblongi, apice paullo attenuati, basi in pedicellum glandula breviorem contracti, satis dense albido-villosuli, stylis siccis exceptis circ. 3.5–4 mm. longi, aperti valvis apice paullo recurvis.

Yunnan boreali-occidentalis: inter oppida Yung-ning et Yung-peh-ting, in pratis ad ripas prope viculum Pi ji, 24 Junii 1914, *C. Schneider* (no. 1646; typus in Herb. Arb. Arn. et Herb. Schneider; frutex ad 4-metralis).

Without having seen male flowers, it is difficult to judge the relationship of this species. It mostly resembles *S. hylonoma* Schn., which may be chiefly

distinguished by its more acuminate leaves with a longer silky pubescence on the under surface, by its somewhat thinner fruiting catkins, its longer gland, and by its longer more deeply cleft styles. The specific name is derived from δίβαφος, "double colored."

In Pl. Wils. **3**:122 I described a *S. isochroma*, referring it to sect. HETEROCHROMAE Schn., but according to further observations I believe that this species represents only a variety of *S. hylonoma;* therefore, I suggest the following combination: S. HYLONOMA var. **isochroma** Schn., n. var.

Alnus (subgenus CREMASTOGYNE [Winkl.] Schn.) **Ferdinandi-Coburgii,** n. sp.—Arbor; ramuli novelli ut videtur dense fulvo-villosulo-tomentelli, annotini plus minusve glabrescentes, atrofusci, lenticellis sparsis flavo-brunnescentibus obtecti, vetustiores nigrescentes; gemmae stipitatae, subglobosae, subglabrae, resinosae. Folia matura chartacea, late elliptica vel subobovato-elliptica, apice satis subito in acuminem brevem producta, basi rotundata vel fere semper cordata, minora 5–7.5 cm. longa, 2.5–4 cm. lata, maxima ad 14:8 cm. magna, margine praesertim ad apicem satis distanter aequaliter breviter glanduloso-denticulato-serrata, superne satis obscure viridia, costa incisa breviter glanduloso-pilosa excepta glabra, nervibus planis, subtus discoloria, glaucescentia, pruinosa et sub microscopio subpapillosa, glandulifera, ad costam nervosque laterales valde prominentes flavobrunneos utrinsecus 12–17 plus minusve fulvo- (et glanduloso-) villosula (novella probabiliter satis dense tomentella) vel fere omnino glabrescentia; petioli crassi, superne sulcati, glanduloso-villosuli, 6–12 mm. longi. Amenta tantum feminea fructifera visa, pro subgenere *Cremastogyne* normalia, ovato-elliptica vel ovato-subglobosa, ad 2 cm. longa et 1.5 cm. crassa, plus minusve resinosa; pedunculi 10–15 mm. longi, laxe villosuli; bracteae ut in tabula fig. K, 2–4 delineatae, apice breviter obtuse lobatae et incurvatae, fere glabrae sed resinosae, circ. 12 mm. longae et (apice) subaequi latae; semina obovato-rectangularia, circ. 4 mm. longa, alis angustissimis cincta.

Yunnan boreali-occidentalis: in montibus Tsang prope Tali-fu, in vallibus ad latera orientalia, alt. circ. 2800 m., 3 Octobris 1914, *C. Schneider* (no. 2716; typus in Herb. Arb. Arn. et Hb. Schneider).

This interesting alder certainly belongs to sect. CREMASTOGYNE Winkler, which I raised to the rank of a subgenus in Pl. Wils. **2**:492. 1916. In many respects it resembles *A. lanata* Duthie, but it may be distinguished from it, as well as from *A. cremastogyne* Burk., by the much shorter peduncle of its fruits, and especially by the almost wingless seeds which are entirely different from

the broadly winged seeds of the two other known species of this group. The male and female flowers of the new species are yet unknown.

As I pointed out (l. c.), the subgenus *Cremastogyne* is a very distinct one, and differs widely from subg. *Alnus* Endl. and *Alnaster* Endl. in its single male and female aments, which appear in the spring on this year's branchlets in the axils of normal leaves. The male flowers are entirely apetalous (fig. K, 6–9), and the female flowers, so far as I can see, agree well with those of the other subgenera; they are shown in fig. K, 10–12. In fig. K, 12, the small "prophylla" of the female flowers can be seen, which are hairy at the apex. In *A. cremastogyne* the female flowers I have seen had always 3 stigmas. The fruiting bracts and the seeds of *A. lanata* are represented in fig. K, 14–16; those of *A. cremastogyne* are very similar.

I take the liberty of dedicating this excellent species to His Majesty King Ferdinand I of the Bulgarians, an eminent botanist and patron of natural history.

ARNOLD ARBORETUM

EXPLANATION OF PLATE XV

FIG. A.—*Salix tenella: 1*, young female flower with bract; *2*, *3*, stigmas; *4*, ventral gland; *5*, dorsal gland; *6*, bract with dorsal gland.

FIG. B.—*Salix Balfouriana: 1*, old female flower with bract; *2*, ventral gland; *3*, bract; *4*, mature fruit.

FIG. C.—*Salix Guebriantiana: 1*, young male flower; *2*, anthers; *3*, ventral gland; *4*, both glands with the base of the filaments between them; *5*, bract with dorsal gland.

FIG. D.—*Salix wolohoensis: 1*, old female flower with bract; *2*, stigmas; *3*, ventral gland; *4*, bract; *5*, ripe fruit.

FIG. E.—*Salix squarrosa: 1*, female flower with bract; *2*, stigmas; *3*, *4*, ventral gland and pedicel of the ovary; *5*, bract.

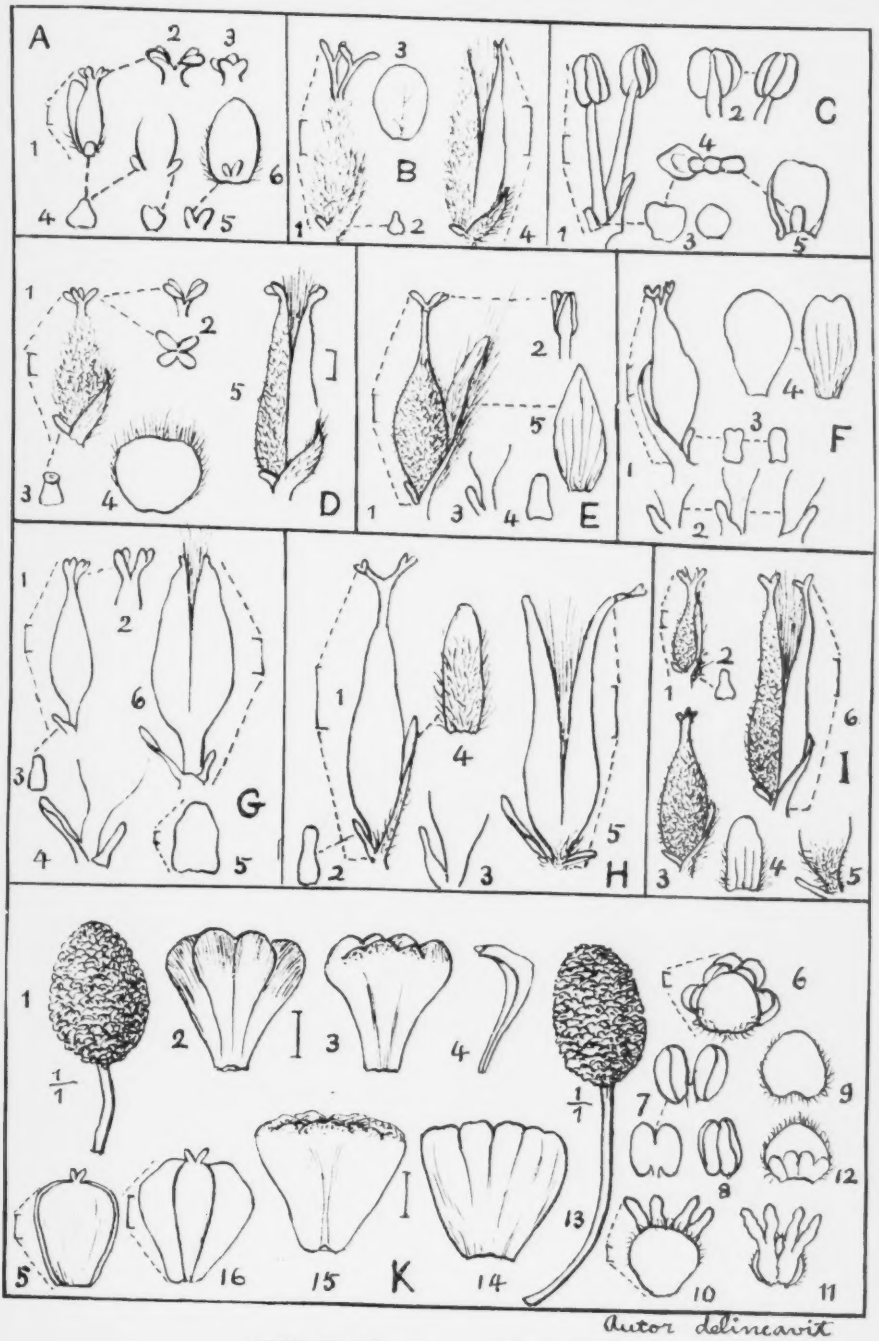
FIG. F.—? *Salix Lindleyana: 1*, female flower with bract; *2*, ventral gland and pedicel of the ovary; *3*, ventral gland; *4*, bract.

FIG. G.—*Salix caloneura: 1*, female flower; *2*, stigmas; *3*, ventral gland; *4*, pedicel of the ovary with bract and gland; *5*, bract; *6*, fruit.

FIG. H.—*Salix Faxoniana: 1*, female flower; *2*, ventral gland; *3*, gland and pedicel of the ovary; *4*, bract; *5*, ripe fruit.

FIG. I.—*Salix dibapha: 1*, young arrested female flower; *2*, its ventral gland; *3*, older female flower; *4*, bract; *5*, base of the ovary and gland; *6*, ripe fruit.

FIG. K.—*1–5*, *Alnus Ferdinandi-Coburgii: 1*, ripe strobile; *2*, fruiting bract ventral; *3*, same dorsal; *4*, same lateral; *5*, seed: *6–16*, *Alnus lanata; 6*, male dichasium with bract (front view); *7*, male flower; *8*, anther; *9*, bract; *10*, *11*, female dichasium with bract; *12*, bract with flowers removed showing their "prophylla"; *13*, ripe strobile; *14*, fruiting bract ventral; *15*, same dorsal; *16*, seed.



SCHNEIDER on CHINESE PLANTS

REPRODUCTION IN THE CONIFEROUS FORESTS OF NORTHERN NEW ENGLAND[1]

BARRINGTON MOORE

This investigation was undertaken to determine the factors governing the reproduction of the more important coniferous trees in the forests of northern New England. A detailed study of a single area was considered more effective than general observations over a wide area, but the study is not by any means exhaustive for the single area.

The work was done on Mount Desert Island, situated toward the eastern end of the coast of Maine, in about the same latitude as the northern part of the Adirondacks and northern New Hampshire. The island is included in the spruce region according to HAWLEY and HAWES (3). This is strictly correct; nevertheless, parts of the island show unmistakable signs of the more southerly white pine region. The location of the island is therefore of unusual interest. Being at the edge of the tension zone between two important regions, each with a distinct flora, there is a good opportunity to determine whether or not the northward migration of plants is still going on, and, if so, to study not only the rate of this migration, but also the many intricate factors involved in this phenomenon. Fortunately, about 5000 acres of this island have been made into a National Park, not only for purposes of recreation, but for scientific research in plant and animal ecology and in forestry.

The island is roughly 12 miles long by 15 miles wide, with a granite core running about northeast and southwest through its southern half. This granite has been cut across by glacial and water action in 9 places, so that instead of a continuous ridge we have a series of small mountains, 7 of them rising to over 1000 ft. above the sea. The northern slopes are gentle, the southern slopes

[1] Delivered at the New York meeting of the Ecological Society of America, December 28, 1916.

are precipitous, due probably to water action during the post-glacial submergence (**5**). The northern half of the island is comparatively level. The topography therefore offers a diversity of habitats.

The climate of the island is a curious mixture of the marine and the inland, the former, of course, predominating, but the latter being found in places shut off from the ocean winds. On the northeast side of the island the average annual precipitation is 48.3 inches, of which 16.1 inches or one-third comes in the growing season (May–September inclusive). This should be abundant, but there are periods during the summer in which lack of moisture is an important factor.

The mean annual temperature is 44° F., running from 21° in January to 65.5° in July. The sea tends to keep the temperature uniform, but it is uniformly cold, for it is beyond the Gulf Stream. There are surprising fluctuations in temperature, however. The large areas of exposed granite rock take up and radiate great quantities of heat, so that the fluctuations, particularly in places cut off from the ocean winds, must have a distinct bearing on the vegetation.

The vegetation, although predominantly northern, contains a strong mixture of middle Atlantic elements. It contains not only plants but forest associations belonging to both the boreal and the transition zones (**4**). Furthermore, this island and Schoodic Point, a small peninsula about 10 miles to the eastward, are isolated stations for *Pinus divaricata*.

The forest associations of the island are 5 in number: (1) spruce, (2) white pine, (3) cedar, (4) pitch pine, (5) grey birch-aspen. Over most of the island, except the parts recently burned, the first 3 associations mingle in a rather confusing manner to form a forest containing varying proportions of red spruce, balsam fir, white pine, and white cedar, with an admixture of red maple, grey birch (giving place to paper birch and yellow birch on the cooler, moister sites), aspen, and occasionally red oak.

1. The spruce association is composed of nearly pure spruce, (*Picea rubens*), mixed with hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and white pine

(*Pinus Strobus*). It occurs on almost any site, even bare rock, provided there is moisture.

2. The white pine association, composed of nearly pure white pine, is not abundant. The association on Mount Desert, although predominantly white pine, contains a strong admixture of red spruce and cedar, and sometimes of red pine (*Pinus resinosa*). It occurs on somewhat drier sites than the spruce association.

3. The cedar association does not form as pure stands as the two preceding ones. Although cedar predominates numerically, there are generally considerable proportions of fir, spruce, and white pine, with red maple (*Acer rubrum*) and paper birch (*Betula papyrifera*). It occupies the moist flats.

4. The pitch pine (*Pinus rigida*) association, generally sharply separated from all others, is composed of pure pitch pine, or sometimes pitch pine and a little red pine. It occupies mostly the dry rocky southern exposures. On rocky flats not exposed to full isolation, white pine, fir, and spruce are creeping in under the pitch pine; on these flats, if not elsewhere, the pitch pine appears to be a pioneer association.

5. The grey birch-aspen (*Betula populifolia–Populus tremuloides* and *P. grandidentata*) association is temporary, following fires, and is replaced sooner or later by the original coniferous forest.

A striking feature of these forests, a feature common to many spruce forests in the west as well as in the east, is the preponderance of fir reproduction under the spruce, even when the parent stand is nearly pure spruce. It is unnecessary to go into the many hypotheses advanced to explain this. Perhaps the most widespread theory, and the one tried out in this investigation, is that the accumulation of acid in the soil under the spruce is detrimental to spruce and favorable to fir. COVILLE's work on the blueberry (**2**) shows that certain plants do require acidity in the soil. Could it be that fir is one of those plants, and that spruce, though tolerant of acid, is not positively benefited by it as the fir appears to be? To determine this point, seedlings of red spruce, balsam fir, and white pine were transplanted from the forest into 3 different kinds of soil. The shoots of these seedlings were measured every 5 days for growth in length. The seedlings were of approximately the

same size and age, and were taken from the same place, so that variations due to size and vigor are eliminated. Each soil was placed in a flat approximately 8 cm. in depth, over which was placed a lath screen made so as to give half shade. All flats were in the open, were given no artificial watering after the first 2 days, and consequently were all under the same conditions except for the soil. These conditions were, furthermore, as close to natural forest conditions as possible.

The 3 soils were (1) A thoroughly decomposed forest humus which had been taken from the forest and rotted in a field for 2 years. This has a moisture-holding capacity, when saturated, of 138.5 per cent of its air-dry weight, or 82.6 per cent of its volume. (2) Undecomposed raw humus, taken directly from the spruce association, consisting of needles, cone scales, and other forest litter. This is COVILLE's "upland peat," the forest "duff" which accumulates in northern regions because decomposition is retarded by lack of sufficient warmth. Its moisture-holding capacity, saturated, is 504.6 per cent of its air-dry weight, but only 65.1 per cent of its volume. The high percentage of water on the basis of air-dry weight gives an idea of the extreme lightness of this raw humus. (3) Mineral soil from beneath the raw humus. This is a bouldery glacial till, a reddish brown sandy loam with but little clay (practically nothing remains in suspension after about an hour and a half). The moisture-holding capacity, saturated, is 66.8 per cent of the air-dry weight and 56.9 per cent of the volume.

It is regretted that the physical properties of the soils cannot be given in terms of the wilting coefficient. The reason is that it was impossible to make wheat or corn produce sufficient root systems in either the raw humus or the mineral soil. On the decomposed humus (soil [1] above) a single direct determination gave a wilting coefficient of 13 per cent. Calculations from the moisture-holding capacity at saturation, which are probably unreliable for these soils, gave, on the basis of volume, wilting coefficients of 21 per cent for the decomposed humus, 15 per cent for the raw humus, and 12 per cent for the mineral soil.

The acidity of each of these soils was tested by the method which COVILLE gives (**2**, pp. 26–28), and by the TRUOG method (**7**).

The decomposed humus was found to be neutral; the raw humus showed an acidity of 0.002 normal, and the mineral soil an acidity of 0.00017 normal by COVILLE's method. Yet by the TRUOG method the raw humus was strongly acid, and the mineral soil of medium acidity. Tests at the end of the growing season showed only a small diminution in acidity.

The measurements showed that the growth of both fir and spruce was most rapid on the mild humus, effectually disposing of the theory that acidity is required by fir, or favors the fir against the spruce. In fact, the difference in rate between the neutral and acid cultures was greater in fir than in spruce, indicating that spruce withstands acidity better than fir. Growth of both fir and spruce on the mineral soil was slightly more rapid than on the raw humus, except that toward the end of the season some of the spruces on the raw humus began a second growth period which enabled them to pass those on the mineral soil. White pine also did better on the mild humus than on the mineral soil; on the raw humus there were not enough trees of this species for definite conclusions.

The duration of the period of growth in length for the different species is interesting. Fir began elongating on June 1, and stopped on July 10, 40 days later; spruce and pine began on June 5, and did not stop until August 20, a period of 76 days, or nearly twice as long as that of fir. Some of the spruce on the raw humus showed a second growth period lasting until August 30; and yet fir, with its shorter growing period, is a faster growing tree than spruce.

An examination of the root systems of the different species on the different soils, made at the end of October, revealed some suggestive conditions. The roots of all 3 species in the mineral soil showed by far the poorest development. Yet the growth curves for the mineral soil show it to have been a little better than the raw humus. It may be that the nutrients contained by the raw humus are considerably less than in the mineral soil. The poor root development on the mineral soil is perhaps attributable to poor aeration. Since this was not a heavy soil, we have here another indication of the need for an ample oxygen supply on the part of the roots of these 3 conifers (1).

The roots of all species were thicker and thriftier looking on the raw humus than on the mild humus, although fir and white pine were a little more branched on the mild humus. Most striking of all, the roots of all 3 species on the raw humus were still capable of absorption, even at the end of October. This was shown by the presence of a considerable number of the little translucent growing tips which are found during the height of the growing season. On the mild humus growing tips capable of absorption were almost lacking except where the root came in contact with the wood of the flat. In the raw humus the root tips which had ceased to function became brown, while many of those on the mild humus became covered with a white fungus. A black fungus, common in the raw humus of the forest, was found attacking the roots on the mineral soil more than those on the raw humus, indicating that its presence may be due to low vigor on the part of the roots rather than to abundance of spores. The rootlets in the raw humus exhibited a propensity for searching out twigs and cones and growing through them.

Raw humus appears to have an effect on damping off fungus, quite the reverse of what might be expected. In an experiment to determine the effect of drying out, such as the raw humus is subjected to under natural conditions in the open, upon the germination and establishment of *Pinus resinosa*, it was found that on raw humus kept artificially moist there was no damping off, while on the raw humus which received no water except from rain the loss from damping off was 44.4 per cent of the seedlings germinating. That damping off should be so much worse on a dry than on a moist soil is contrary to all previous experience. The explanation is probably to be found in the great abundance of fungus spores in raw humus as compared with ordinary nursery soils, and in the much greater vigor and power of resistance on the part of the seedlings in the moist humus. It is also possible that the constant moisture held enough of the soil acid in solution to prevent germination of the damping off fungus spores, for it is known that treatment of nursery soils with acids before seeding, followed by ample watering during germination, diminishes the losses from damping off.

Experiments were also tried on the effect of these 3 soils on the growth of clover, wheat, and corn. Clover, as might be expected from its sensitiveness to acid, grew very poorly on the raw humus and mineral soil, but throve on the mild humus. In fact, it eventually died back and disappeared on the two former, lasting longer on the mineral soil than on the raw humus. Kubanka wheat did well on the mild humus, except for the shading, while on the raw humus and mineral soil it grew poorly. The dry weights per plant for Kubanka wheat sown June 24 and cropped September 15 were 0.53 gm. for the mild humus as against 0.08 gm. on the raw humus, and only 0.03 gm. on the mineral soil. Corn (Golden Bantam) did so well on the mild humus that it had to be removed to prevent interference with the other experiments, while on the raw humus it produced only 0.09 gm. dry weight per plant, and on the mineral soil 0.13 gm. after growing for more than 3 months. The corn, it will be noticed, did better on the mineral soil than on the raw humus, indicating that this plant is affected more by acidity than by poor aeration. On the other hand, wheat grew better on the raw humus than on the mineral soil; on the former it frequently died down but came up again, while on the latter it showed less power of recovery. This would indicate that wheat is less sensitive to acid than to poor aeration.

Field observations on the root systems of spruce, fir, and white pine showed that detailed studies of roots would probably yield interesting results. Spruce roots form a dense mat in the raw humus or "duff," a mat so dense that hardly a square centimeter under a spruce stand escapes. These rootlets keep growing toward the surface as the humus deepens, those in the lower layers dying back. Hence spruce is in a position to get the first water that reaches the forest floor. The quantity absorbed by these roots must be enormous, and cannot fail to be an important factor in reproduction. Fir roots are characteristically much less branched than those of spruce, and seem to go more into the mineral soil, though they also feed largely in the "duff." This greater penetration may possibly explain in part the ability of fir to grow on drier sites than spruce. White pine absorbs from both the raw humus and the mineral soil. The roots of all 3 species are often

affected by a fungus which produces black threads of mycelium on the root tips. These threads prevent absorption and kill the portion of the root attacked. Yet seedlings appear thrifty even when a large proportion of their roots are affected in this way. Perhaps, since the fungus attacks only the smaller rootlets, the plant is able to develop new rootlets about as fast as the affected ones die off.

A factor of more importance than hitherto recognized is dryness due to the interception of precipitation by the crowns of spruce. The lack of vegetation under a forest of spruce has generally been attributed to lack of light. While light plays an important part, there are probably many cases where lack of moisture rather than lack of light is the determining factor. A rather striking illustration may be cited. Under the crown of a spruce growing in the open was found a patch of forest floor similar in every respect to the forest floor found under dense stands of spruce. Herbaceous vegetation and tree reproduction stopped abruptly at the edge of this spot, yet the crown of this tree was high enough to allow the ground under it to receive ample light. The only vegetation under the crown was a few grasses and asters, light demanding but comparatively drought resistant plants. The bareness of this piece of forest floor was due to lack of moisture, not to lack of light. This was confirmed by moisture tests, which showed that the soil beyond the crown, soil which had been giving up moisture to a thick herbaceous cover all summer and should consequently be drier than a spot which had given up nothing to vegetation and was not subject to high evaporation, possessed 59 per cent of moisture on the basis of air-dry weight as against 20.5 per cent under the crown of the spruce. On the basis of volume, which gives a better conception of the moisture relations in these light soils, the soil in the open contained 19 per cent of moisture as compared with 5.7 per cent under the crown. In another case in a spruce forest the moisture under a small opening in the canopy was 20.9 per cent by volume, as compared with 7.3 per cent under a spruce crown. In both of these cases the soil under the crown was powder-dry to the touch, while that beyond the crowns felt moist. It is evident, therefore, that under the crowns of spruce the soil is

often so dry that neither reproduction nor herbaceous vegetation can become established, no matter how much light it receives.

Counts of the reproduction of spruce, fir, white pine, and cedar, correlated with age, showed that spruce, fir, and white pine become established only at intervals of several years, while cedar comes in every year. The cause of the failure of spruce and fir to become established every year is apparently not related directly to climatic factors, because the season of 1916 was unusually moist and favorable, yet practically no seedlings of these 2 species could be found. Probably the reason for this periodicity in spruce and fir reproduction is to be sought largely in the seed supply. White pine reproduced abundantly in 1916, so that climate can be eliminated as a factor; but since it is equally impossible to eliminate the matter of seed production, the periodicity of white pine reproduction may be due to both the season and the seed supply.

In fir there are indications of a periodicity of reproduction which is of considerably more importance than that due to the seed supply. Under many spruce stands which have reached about middle age, the fir reproduction is nearly all composed of large seedlings approximately 1–3 ft. in height; young seedlings are scarce. In these cases it appears that the fir came in profusely under a set of environmental conditions different from the present ones. Just what these conditions were it is impossible to say without further study. One of them may have been stronger light than at present. Indications of this were found in the fact that some of these cases of fir reproduction occur in stands which were formerly more open than they now are; also, small fir reproduction is abundant in young stands with a full but not very heavy canopy. That light is a factor would be in accordance with ZON's conclusion (**8**). Another factor may be decreasing moisture, due to the interception of precipitation by the crowns of the spruce trees, and to a fuller use of the humus water by the increasing mat of spruce roots. Whatever the factors are, it seems evident that fir reproduces within a more or less sharply marked range of environmental conditions, and that these conditions are largely controlled by the forest itself.

Each species reproduces only within a certain range of factors. This range is probably a specific characteristic of each tree, possibly of each plant, and appears to be different even for trees growing together in the same association.[2] Determination of this range for even a few of our more important trees would be a valuable contribution.

NEW YORK CITY

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[2] SHREVE (6) found that in open vegetation in Arizona the species growing in the same association are subject to different environments.

POLLEN TUBE AND SPERMATOGENESIS IN IRIS

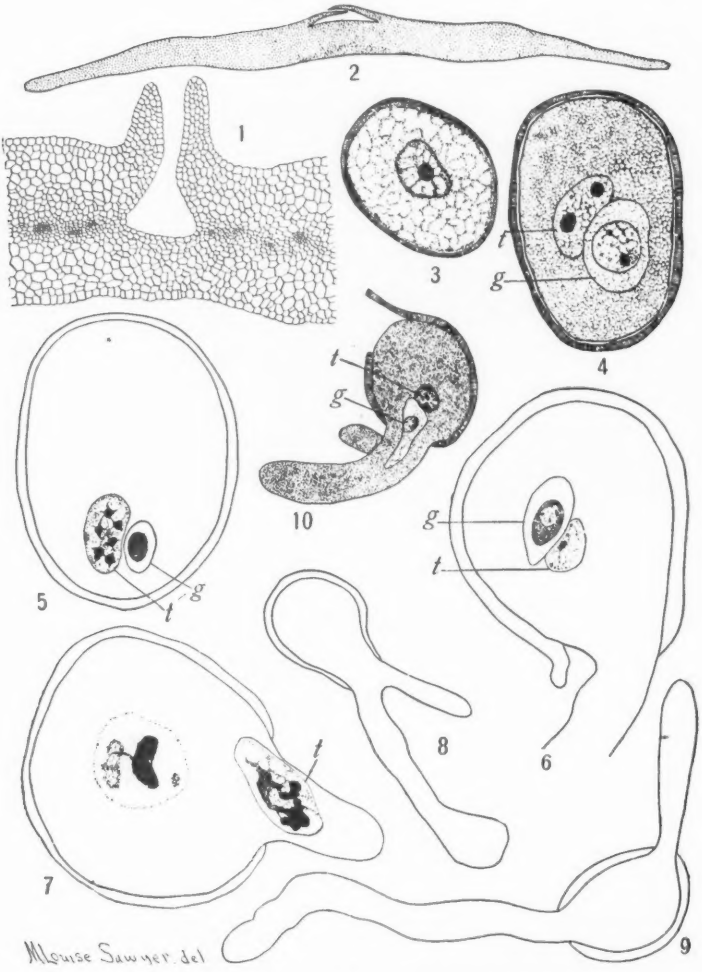
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 235

M. Louise Sawyer

(WITH EIGHTEEN FIGURES)

This study of spermatogenesis had its origin in an attempt to find a satisfactory method of securing prepared as well as living material for demonstrating pollen tubes to a class in embryology. The fact that it was found possible to dissect out the pollen tubes of *Iris versicolor*, so that tubes of various lengths, developed on the stigma and style, became available for study, made it seem advisable to undertake an investigation of the pollen tube of this species. Tubes were also secured in longitudinal sections of style and stigma, and by sowing pollen grains on culture media. Tubes were grown in sugar solutions, the 15–30 per cent proving more satisfactory than weaker solutions. A culture medium was made by adding 30 per cent sugar solution to the sap which oozes from freshly cut stalks, and abundantly from the clasping bases of the leaves. The superiority of the latter over the pure sugar solution lies in the fact that as the tubes grow longer they are less likely, in the cell sap sugar solution, to become distorted. Its disadvantage consists in the difficulty of freeing the tubes from the gelatinous medium.

Flemming's stronger solution proved the most satisfactory killing fluid, and iron-hematoxylin has been the favorite stain. The successful dissection of the tubes is related to the structure of the style. That organ arises from the ovary as a single structure, and at the height of about 1 cm. divides into 3 branches. Cross-sections of a stylar branch (fig. 1) reveal the fact that each branch is traversed by a longitudinal groove. When the flower is mature, the stylar groove is covered by two overlapping outgrowths, arising from the margin of the groove and so forming an inclosed canal, diagrammatically shown in fig. 2. Near the distal end the groove broadens out and terminates in the stigma, which appears as a shelflike projection from the under side of the stylar branch, which



FIGS. 1–10.—Abbreviations are as follows: *t*, tube nucleus; *g*, generative cell; *m*, male cell; *e*, egg; fig. 1, transverse section of young stylar branch, showing groove through which pollen tubes grow, ×124; fig. 2, diagram of mature stylar branch, in transverse section, showing groove covered; fig. 3, young pollen grain, ×1113; fig. 4, mature pollen grain from section of anther, ×1113; fig. 5, pollen grain sectioned on stigma, showing end view of tube nucleus and generative cell, ×1113; fig. 6, pollen grain and tube grown on stigma, tube nucleus and generative cell being still within the grain, ×1113; fig. 7, pollen grain with short tube into which tube nucleus is passing; generative cell poorly defined, still in center of grain, ×1113; fig. 8, pollen tube grown in sugar solution, showing branching tube, ×540; fig. 9, pollen tube grown in sugar solution, showing 2 tubes from a single grain, ×540; fig. 10, pollen grain (*pg*) of fig. 11, showing generative cell in act of entering tube, tube nucleus following, ×540.

is continued beyond the stigma. By removing the covers of the groove the canal containing the tubes lies exposed, and they can be removed with needles.

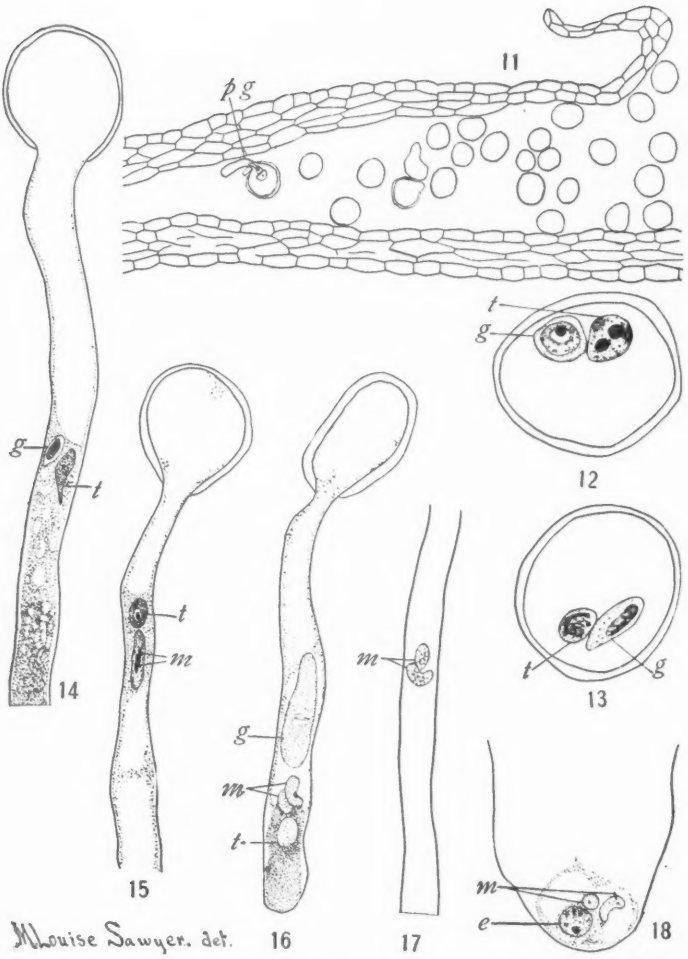
Tubes grown in hanging drops of culture media show a rather striking tendency to grow from the margins of the drop in groups, the tubes being in close contact with each other. This fact is suggestive when associated with the fact that from the stigma the pollen tubes converge in two lines and traverse the stylar branch at the margins of the groove, where the space is most restricted (fig. 2). It has usually been assumed that the pollen tube is guided in its direction of growth by chemotaxis. These observations suggest that in *Iris* contact stimulus may be an effective guide. Further investigation of this point is purposed.

The structure of the newly formed pollen grain (fig. 3) was studied in sections of the anther. The division of the microspore nucleus was not observed, but it occurs in the anther, as would be expected, and the generative cell is organized before dehiscence (fig. 4). The generative cell is slender, elongated, and somewhat pointed when seen from the side (figs. 6, 13), and is frequently overlaid by the tube nucleus (figs. 4, 5). In this condition the pollen is shed. Hand pollination was successfully performed. Usually cross-pollination was effected, but it was demonstrated that pollen would produce abundant tubes on the stigma of the stylar branch under which it was located. Observation on the rate of growth of pollen during 7 hours after pollination was made, and their lengths measured with an ocular micrometer. Table I indicates results.

TABLE I

Time after pollination	Length of tubes
1 hour	0.1–0.6 mm.
3 hours	2–2.5
5 hours	4.5–5
7 hours	8–9.5

The acceleration in the rate of growth, as indicated by these data, is interesting. In 9–10 hours tubes were observed at the base of the stylar branch. After 20 hours tubes were discovered



FIGS. 11–18.—Abbreviations are as follows: *pg*, pollen grain; *t*, tube nucleus; *g*, generative cell; *m*, male cell; *e*, egg; fig. 11, section of stigma with pollen grains, some of which are growing tubes, ×140; figs. 12 and 13, pollen grains in anther, showing appearance of tube nucleus and generative cell from different views, × 1113; fig. 14, pollen tube with tube nucleus in act of passing generative cell, ×540; fig. 15, pollen tube with generative cell containing 2 male nuclei preceding tube nucleus, ×540; fig. 16, pollen tube with tube nucleus and 2 male nuclei near tip, expanded cytoplasm of generative cell above showing cavities from which male nuclei escaped, ×540; fig. 17, portion of a long pollen tube, showing 2 male nuclei free in tube, ×540; fig. 18, end of embryo sac, with egg and 2 male nuclei, ×540.

within the ovary. The pollen tubes occasionally branch. This was observed both in tubes grown on the stigmas and in those grown on nutrient solutions (fig. 8). In the cell sap sugar solution some grains produced 2 tubes (fig. 9), indicating 2 germination spots.

Longitudinal sections of hand pollinated stigmas (fig. 11) show pollen grains (fig. 5) which have essentially the characteristics of the grains in the dehiscing anthers, and among them grains which are producing pollen tubes. A tube (fig. 10) caught just as the tube nucleus and the generative cell were passing the tube distinctly shows the latter preceding, contrary to the order that is usually reported. In other cases the tube nucleus led the way from the grain into the pollen tube (fig. 7). The number of cases thus far observed at just this stage is not sufficiently large to warrant a statement as to which of these conditions is prevalent in *Iris versicolor*. Apparently it is usual for the tube nucleus to soon gain the leading position. One instance (fig. 14) of the tube nucleus in the act of passing the generative cell was observed. The peculiar elongated and pointed anterior end of the tube nucleus is very interesting and suggests a self-motile body.

The generative cell certainly usually passes into the tube before its nucleus divides to form the male nuclei, but occasional grains suggest the possibility that it sometimes divides in the grain. The division of the generative cell has not been observed, but in tubes dissected from the stigma, and in those grown in the culture media, the generative cell has frequently been seen apparently containing 2 nuclei (fig. 15*m*). The contents, which microchemical tests show contain much starch, stain so heavily that it is difficult to differentiate the nuclei satisfactorily. The material seems to indicate a somewhat wide range in the position of the generative cell in the tube at the time division of its nucleus occurs.

A tube (fig. 16) but a fraction of a millimeter in length appeared to contain the tube nucleus, behind it the generative cell cytoplasm, and between them, free in the tube, the 2 male nuclei. In a group of dissected tubes which were about 14 mm. long, a tube contained free male nuclei (fig. 17) about halfway between the grain and the end of the pollen tube. At 79 hours after pollination such male nuclei were seen in the embryo sac (fig. 18). It is noticeable that

in all of these cases no cytoplasm could be detected in association with the male nuclei, and also that in all views of these male nuclei one of them appears larger than the other, the larger one slightly vermiform. It remains to determine whether this apparent difference is real or whether in each case one of the nuclei is seen from the end. In the embryo sac section it seems probable that the smaller appearing one is the one likely to fertilize the egg.

Summary

1. The style of *Iris versicolor* is traversed by a longitudinal groove through which the pollen tube grows.

2. It is possible to remove pollen tubes from style and stigma and to grow pollen tubes in nutrient solutions.

3. Measurements indicate that there is an accelerated rate of growth of pollen tubes.

4. Pollen tubes may branch or a grain may produce two tubes.

5. The generative cell is an elongated, somewhat pointed cell, and may precede the tube nucleus from the tube.

6. Production of the male nuclei usually occurs after the generative cell has entered the tube.

7. The male nuclei may leave the generative cytoplasm, and were seen free in the tube.

8. The male nuclei were observed in the embryo sac 79 hours after pollination.

The writer is indebted to Professor H. D. DENSMORE of Beloit College for suggestions which led to the undertaking of this investigation. Acknowledgments are also due Professor JOHN M. COULTER and Dr. CHARLES J. CHAMBERLAIN for helpful criticism during the progress of this work.

BELOIT COLLEGE
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BRIEFER ARTICLES

ELLSWORTH JEROME HILL

(WITH PORTRAIT)

E. J. HILL was a well known figure to the Chicago group of botanists. For over 40 years he studied the plants of the Chicago region. No one was more familiar with them, or had brought so many of them to general notice. He was much more than a collector and taxonomist; in addition, he was an ecologist before ecology was recognized as a subject.

He was born at LeRoy, New York, December 1, 1833, and died in Chicago, January 22, 1917. His early life was spent on a farm, in which environment he began to develop his love of natural history. At the age of 19 he was taken suddenly lame by an affection of the knee, and during the rest of his long life, with intervals of relief, this trouble accompanied him. After his first trouble, to get away from the northern winter, he went to Mississippi and taught for three years in a woman's college at Grenada, afterward returning to New York. In 1860 he began a theological course in Union Theological Seminary, graduated in 1863, and engaged in pastoral work until 1869, when another attack of lameness incapacitated him for two years. He then became a teacher again, first in the high school of Kankakee, Illinois, for four years, and then for fourteen years in the high school of Englewood, now a part of Chicago. In 1888 he gave up teaching and devoted himself almost entirely to botany.

Hill's experience as a persistent field student is a lesson in patience and courage. His numerous field trips on crutches and afterward with canes; his devices to overcome the handicap of lameness while collecting; his persistence in making these trips even when he paid a severe penalty for exposure or over-exertion—all testify to the spirit of the man. During his later years he was a constant and welcome visitor at the weekly meetings of the Botanical Club of the University of Chicago, and was always intensely interested in the various phases of modern botany. His mind was open and progressive, turned toward the future of his subject rather than toward the past.

His bibliography as published includes 162 titles, ranging in time from 1870 to 1916, and covering all the phases of botany that would attract the attention of an active field man with broad interests. This journal published 34 of his titles, the majority of them during the decade 1880–1890, and the last one in 1910. Certain genera received his critical attention, among them being *Potamogeton*, *Carex*, *Quercus*, *Prunus*, *Salix*, and *Crataegus*. Taxonomists will recognize the fact that these are difficult genera, but it was their difficulty that attracted.

The Hill Herbarium, which is said to include 16,000 sheets, the accumulation of years of critical work, has been secured by the University of Illinois. It represents probably the most valuable single collection of Illinois plants, especially of the Chicago region, and it is fortunate that it has been made available in a public institution.—J. M. C.

RESISTANCE OF SEED COATS OF ABUTILON THEOPHRASTI TO INTAKE OF WATER

In the fall of 1910 I gathered seeds of *Abutilon Theophrasti* (velvet leaf) near Manhattan, Kansas, placed them in vials of 100 seeds each, covered them with water, and stoppered the vials. The results in the various vials up to the present time have been very similar.

In one vial 32 seeds had swollen within the first 3 weeks and were removed from the vial. During the past 6 years 22 of the remaining seeds have swollen and were removed, sometimes in a decaying condition, as the vial was seldom examined. In December 1916 a desk in which the vial was stored was removed to a small room and placed near a radiator where the temperature rose much higher than any to which the seeds had previously been subjected. Within a week 22 seeds had swollen. These were removed and placed under germinating conditions

and germinated as quickly and apparently with as much energy as fresh seeds. Of the original 100 seeds 24 still remain intact.

In order to ascertain the resisting power of the seed coats of velvet leaf to water at various temperatures, in December 1916 I collected seeds from plants still standing in the field. Most of the seeds at that time had dropped from the pods, and those I found were mostly hard-coated. In one case only 3 seeds in 100 had swollen after soaking 48 hours at room temperature. Two lots of seeds of 100 each were selected and each lot was placed in a small vial. The vials were then filled with water at a given temperature and suspended in Dewar flasks filled with water at the same temperature. At the end of 6 hours the vials were removed, the seeds that had swollen were counted, removed, and the remaining seeds were returned for a similar period at a temperature 5° higher, and so on until all the seeds had swollen. The temperature of the flask for each period was kept practically constant. The seeds in flask no. 1 were started at 30° C., and in no. 2 at 35° C. The results are indicated in table I.

TABLE I

Flask no. 1			Flask no. 2*		
Temperature	Time in hours	Number swollen	Temperature	Time in hours	Number swollen
30° C.	6	8	35° C.	6	15
35	6	9	40	6	13
40	6	19	45	6	12
45	6	17	50	6	13
50	6	8	55	6	13
55	6	5	60	6	9
60	6	12	65	6	10
65	6	7	70	6	5
70	6	10	75	6	4
75	6	5			
Total		100	Total		94

*6 seeds were lost.

These results indicate a wide range in the resisting power of the coats of these seeds to the intake of water, and no doubt many of the more resistant may lie in the soil many years before germination can take place.—Wilmer E. Davis, *Kansas State Agricultural College.*

CURRENT LITERATURE

BOOK REVIEWS

Contributions to plant physiology

In a little booklet[1] of 95 pages is given the work of the department of plant physiology at Johns Hopkins University. LIVINGSTON gives a description of the department, discussing the aims and the work in progress or so far accomplished, to which is appended a list of the publications from the laboratory arranged by years. The rest of the book is devoted to abstracts of work in progress or recently completed. A list of the authors and titles of these articles will give an idea of the number of investigators in the department, along with the nature and scope of the problems being covered: B. E. LIVINGSTON, Atmometric units; The vapor tension deficit as an index of the moisture condition of the air; Incipient drying and temporary and permanent wilting of plants, as related to external and internal conditions; B. E. LIVINGSTON and E. E. FREE, The effects of deficient soil oxygen on the roots of higher plants; E. E. FREE, The effect of aeration on the growth of buckwheat in water cultures; Symptoms of poisoning by certain elements in *Pelargonium* and other plants; E. E. FREE and S. F. TRELEASE, The effects of certain mineral poisons on young wheat plants in three-salt nutrient solutions; The effect of renewal of culture solutions on the growth of young wheat plants in water cultures; S. F. TRELEASE, The relation of the concentration of the nutrient solution to the growth of young wheat plants in water cultures; H. S. FAWCETT, Preliminary note on the relation of temperature to the growth of certain parasitic fungi in cultures; The geographical distribution of the citrus diseases melanose and stem-end rot; HOWARD PULLING, Some unusual features of a sub-arctic soil; The experimental determination of a dynamic soil-moisture medium; F. M. HILDEBRANDT, Leaf product as an index of growth in soy bean; A method for approximating sunshine intensity from ocular observations of cloudiness; F. S. HOLMES, Moisture equilibrium in pots of soil equipped with auto-irrigators; E. S. JOHNSTON, Seasonal variations in the growth rates of buckwheat plants under greenhouse conditions; W. E. TOTTINGHAM, On the relation of chlorine to plant growth.

Aside from many individual contributions, the work of the laboratory groups itself largely about three large topics: water relations of plants, inor-

[1] Contributions to Plant Physiology, the Department of Plant Physiology, Johns Hopkins University, Reprint from the Johns Hopkins University Circular, March 1917.

ganic salt relations of plants, and relation of plants to climatic conditions. A quotation from the book expresses the point of view under which the work of the laboratory is being conducted.

To summarize the last few paragraphs, our operations have been and are directed toward a dynamic analysis of plant activity. The point of view here employed may perhaps be envisaged if the reader will regard the living plant in somewhat the same general way as he might any complex machine, such as a gasoline motor, for example. To understand its working, one must understand how and how much various conditions may effect a machine; in short, he must become an engineer with respect to that particular mechanism. Dynamic plant physiology may be said, then, to be engineering science as applied to the living plant. It can progress, then, only through quantitative studies, through the comparison of efficiency graphs and curve-tracings made by recording instruments, through the mathematical interpretation of relations between conditions and process rates, etc., and it is with just this sort of studies that our investigations have to do.

It might be well if scientific departments generally issued such statements of their aims and progress.—WM. CROCKER.

NOTES FOR STUDENTS

Rhizoctonia.—In a paper constituting a continuation of former studies of the genus *Rhizoctonia*, ERIKSSON[2] adds an account of two further forms, *R. Medicaginis* DC. and *R. Asparagi* Fuckel. The paper deals largely with historical and descriptive matter; the chief interest, however, centers in the questions relating to the taxonomy and morphology of these fungi. In 1851 the TULASNE brothers united *R. crocorum* DC., *R. Medicaginis*, and most of the forms of *Rhizoctonia* occurring on other hosts under one species, which they called *R. violacea* Tul. ERIKSSON, basing his judgment partly upon the association of *Leptosphaeria circinans* (Fuckel) Sacc. with *R. Medicaginis* reported in the literature and also observed by him, and partly on the resemblance of the hyphae of the germinating spores of *Leptosphaeria* to the mycelium of *Rhizoctonia*, concludes that *Rhizoctonia Medicaginis* has an ascogenous fruiting stage and therefore is distinct from *R. violacea*, which he had doubtfully associated with *Hypochnus violaceus* (Tul.) Erikss. Regarding the specificity of *R. Asparagi*, ERIKSSON concludes, as a result of cross-infection experiments conducted by means of infected soil in deep concrete frames, that this fungus is probably a distinct form whose position cannot be determined until something is known of the perfect stage.

DUGGAR,[3] in a paper published almost simultaneously with that of ERIKSSON, confirms the view of the brothers TULASNE that all the forms of the violet

[2] ERIKSSON, J., Fortgesetzte Studien über *Rhizoctonia violacea* DC. Arkiv. Bot. **12**:1–31. 1915.

[3] DUGGAR, B. M., *Rhizoctonia crocorum* (Pers.) DC. and *R. Solani* Kühn (*Corticium vagum* B. and C.), with notes on other species. Ann. Mo. Bot. Gard. **1**:403–458. 1915.

root-felt fungus found on crocus, alfalfa, and many other hosts (of which 54 are listed by him) belong to a single species, to which the name *Rhizoctonia crocorum* (Pers.) DC. must be applied as long as the fruiting stage remains unknown. This view is based upon a critical examination of the data in the literature and an extensive study of living material and herbarium specimens. He regards the evidence thus far presented as insufficient for the identification of the perfect stage of the fungus. Unlike ERIKSSON, he finds no resemblance between the mycelium produced by spores of *Leptosphaeria circinans* which he germinated and the hyphae of *R. crocorum*. DUGGAR further gives an account of *Rhizoctonia Solani* Kühn, which is the more common of the two species in America where it is the widespread cause of "damping off" of seedlings and cuttings and root-rot of various crops. This species is clearly differentiated from the violet *Rhizoctonia* by characteristics of the mycelium and the sclerotia, as well as by the effects produced on the host plants. Furthermore, evidence seems to be sufficient that the perfect stage of this organism is *Corticium vagum* B. and C. In a later paper,[4] as a result of a study of the data in the literature, this fungus is identified with the "Vermehrungspilz" common in the seed beds and cutting beds of Germany and France, and also with the "Mopopilz," causing considerable damage to the seed beds of cinchona in Java. The failure to recognize *Rhizoctonia Solani* as the general cause of the "damping off" of seedlings in Germany and France, as well as in Java, is attributable to wrong determinations of the European seed bed fungus and the cinchona fungus of Java.

Among other differences mentioned by DUGGAR between *Rhizoctonia Solani* and *R. crocorum* is the difference in their capacity for growing on artificial media. *Rhizoctonia Solani* grows readily on all the common culture media, while *R. crocorum* had not, up to that time, been successfully grown. Recently, however, DIEHL[5] reports successful cultures of the fungus from detached masses of mycelium. The fungus grew with extreme slowness, and only in one instance was a pure culture obtained.

A thorough and comprehensive study of the parasitic Rhizoctonias of the United States has been reported by PELTIER.[6] The chief features of the report are (1) a general historical account, (2) a discussion of the morphology of the fungi, (3) a complete tabulation of the data relating to the hosts, occurrence, and distribution of *R. Solani* and *R. crocorum* in the United States, with notes on the distribution of these organisms in other countries, (4) a description of the disease induced by these fungi in different plants, (5) the results of

[4] DUGGAR, B. M., *Rhizoctonia Solani* in relation to the "Mopopilz" and the "Vermehrungspilz." Ann. Mo. Bot. Gard. **3**:1–10. 1916.

[5] DIEHL, W. W., Notes on an artificial culture of *Rhizoctonia crocorum*. Phytopathology **6**:336–340. 1916.

[6] PELTIER, G. L., Parasitic Rhizoctonias in America. Univ. Ill. Agric. Exp. Sta. Bull. **189**:279–390. *figs. 23*. 1916.

cross-infection experiments with *R. Solani*, and (6) a description of the growth of this fungus in various media.

The numerous cross-infection experiments carried out with *Rhizoctonia Solani* are of special interest. Strains of the fungus from some 30 species of plants were used to infect carnations in several stages of growth, from the cutting to the mature plant, both under glass and in the field. A number of other plants also were infected with various strains of *Rhizoctonia*. The results of all these cross-infection experiments can best be stated in the author's own words: "From these inoculation experiments with a large number of different types of plants, we must conclude that all the strains studied, which were obtained from a wide range of hosts of diverse geographical origin, can attack the same species of plant and produce the same characteristic symptoms. No marked specialization was noted in any of the strains. Thus, all the strains studied can be included under one form, *Rhizoctonia Solani* Kühn. The inoculation experiments show further that the virulence of *R. Solani* is very variable, as is also the degree of resistance of the various host plants, both depending upon a number of factors." A study of the growth characteristics confirmed this general conclusion. Strains isolated from the same host species showed differences as great as those between strains isolated from different species.

MATZ[7] has described a form of *Rhizoctonia* occurring on the leaves and stems of *Ficus Carica* at Gainesville, Florida. This form is regarded by him as a distinct species, *R. microsclerotia* Matz. Aside from its foliicolous habit, it does not appear to differ essentially from *R. Solani*, which MATZ found was also capable of infecting fig leaves, without producing sclerotia, however. In a single experiment the fig fungus failed to infect seedlings of the cowpea, while *R. Solani* killed 90 per cent of the young plants.—H. HASSELBRING.

The number of chromosomes.—Partial lists of the number of chromosomes reported by various observers for various plants have been published from time to time, but the lists have been incidental and usually no authority has been cited. The most complete of these earlier lists is that of TISCHLER (Progressus Rei Botanicae **5**:164–284. 1915). ISHIKAWA[8] has compiled the most complete list ever published, and in each case has cited the authority. Besides, he has counted the chromosomes in several forms which are here reported for the first time. The theoretical interpretation of chromosomes and their value in phylogenetic studies will be considered later. In sexual forms, the x and $2x$ numbers are cited in separate columns; in asexual forms, the numbers are cited in the x column.

A mere glance at ISHIKAWA'S tables reveals some interesting facts. In the Flagellates most of the numbers are preceded by the sign $\pm$, indicating an

[7] MATZ, J., A *Rhizoctonia* of the fig. Phytopathology **7**:110–117. 1917.

[8] ISHIKAWA, M., A list of the number of chromosomes. Bot. Mag. Tokyo **30**: 404–448. *figs. 32*. 1916.

estimate rather than an exact count. All of the Myxomycetes show 8 as the *x* number; in the diatoms only 3 genera are cited, the *x* numbers being 4, 8, and 64, the latter with 128 as the *2x* number; in the Conjugatae 12 is the prevailing number, and in most cases the *2x* is not cited; in the Chlorophyceae the *x* numbers are various, ranging from 6 to 32, but no *2x* numbers are given; in the Phaeophyceae the *x* numbers are 16, 18, 22, 24, and 32, with the expected *2x* numbers; in Characeae the *x* numbers are 21 and 16, but no *2x* numbers are cited; in Rhodophyceae 8 forms are given, with *x* numbers ranging from 7 to 24 and with the corresponding *2x* numbers. In the fungi the numbers are low and the *2x* numbers are given in comparatively few cases; the minimum *x* number is 2, and it has been noted in 2 species; 4 appears in 24 species; very few have more than 8 as the *x* number; and the maximum number (16) is cited in 6 cases. In the bryophytes 8 is the prevailing *x* number, having been noted in 12 species, while 4 has been counted in 6 species, and 12 in one case and 6 in another. The *2x* numbers have been counted in nearly all cases. In the mosses the *x* number ranges from 6 to 24, with 6 (counted in 6 species) as the prevailing number. In the pteridophytes the numbers are comparatively high, the *x* number ranging from 4 to 120, and 24 of the 35 species cited have 32 or more, while only one (*Salvinia*) shows the minimum number. In the gymnosperms 12 and 24 have appeared so constantly as the *x* and *2x* numbers that any other countings need to be very thoroughly supported; 34 species with 12 as the *x* number are cited, and 3 which are cited as having 8 chromosomes are now known to have 12, but there are still 6 species in which the number 8 has not been disputed. Other numbers are 6, 10, and 16. Of the 44 pages of citation, 28 are devoted to angiosperms. The *x* number ranges from 3 in *Crepis virens* to 45 in *Chrysanthemum arcticum*. The average number is higher in the dicotyledons than in monocotyledons, and the most frequent *x* numbers are 8, 12, and 16.

The list is valuable not only for the systematically arranged citations of chromosome counts, but also because it brings together a considerable portion of the cytological literature in which the chromosome appears either as a principal or as an incidental feature.—CHARLES J. CHAMBERLAIN.

Stomatal regulation.—From rather extensive experimentation upon ivy and laurel (*Prunus Laurocerasus*), DARWIN[9] concludes that transpiration is regulated by size of stomatal aperture, and that "LLOYD'S dictum 'their (stomates) regulatory function is almost nil'" must be abandoned. The stomatal aperture was determined by use of his well known potometer, which determines the rate of flow of air through the stomates under a given pressure. The rate of transpiration was determined by weighing or by use of the potometer. Modification of stomatal aperture was induced by normal daily changes or

[9] DARWIN, F., On relation between transpiration and stomatal aperture. Phil. Trans. Roy. Soc. London B **207**:413–437. 1915.

by shorter periods of darkness and light. Humidity of the air was figured to a standard.

Potometer determination of stomatal aperture involves mass movement of air through the stomates under differential pressure, while transpiration involves static diffusion of water vapor through the stomates. To clear up the physics of the problem, DARWIN gives two quotations from Sir J. LARMOR: "The speed of diffusion through a narrow aperture between two open spaces is proportional to its diameter. The speed of a stream of air through such an aperture, between open spaces having different pressures on them, is proportional to its area if the effect of viscosity can be neglected, but proportional to the $\frac{3}{2}$ power of its area if viscosity is preponderant. Which of these conditions prevails, or whether the circumstances are intermediate, in a given case, depends upon the diameter of the aperture." "Diffusion through a long pipe or channel varies as the area, and flow through it depends upon a reduced area owing to the flowing air adhering to the walls of the tube; in fact it varies as the square of the area if viscosity is predominant. Thus if this be the case, provided the channels are of fairly uniform width, transpiration would be proportional to the square root of flow, the same law as that obtained for the case of holes in a thin plate." DARWIN believes the second assumption most nearly represents the situation, for the first applies only to tubes whose lengths are less than one-fifth of their diameter. As might be deduced from either of the physical laws just stated, the author has made one curve by plotting the square root of the rate of potometer flow, and another by plotting the rate of transpiration for various stomatal apertures, and for 18 separate experiments finds general agreement between the curves, although there are many minor discrepancies.

One regrets that the experiments were not carried out in closely controlled temperature and humidity conditions, which might go far to eliminate minor discrepancies. Evaporimeter records and measured light intensities might also aid in explaining these discrepancies. Much has been done since 1900 to put the material and energy exchanges between the leaf and the air upon a sound physical basis, and this is a noteworthy step in that direction. One is impressed by the excellent scientific spirit of the writer, and by the considerate way in which he deals with those who differ from him.—WM. CROCKER.

Sweet potatoes during storage.—HASSELBRING and HAWKINS[10] made a study of the course of the carbohydrate transformations in sweet potatoes (*Ipomoea Batatas*) during storage. The data indicated that a more rapid transformation of starch into sugar took place immediately after the roots were dug than at subsequent periods. This suggested intensive investigation relative to the effect of cessation of leaf activity and the effect of different temperatures on the progress of carbohydrate transformations. The study was

[10] HASSELBRING, H., and HAWKINS, L. A., Carbohydrate transformations in sweet potatoes. Jour. Agric. Research 5:543–560. 1915.

planned so as to include 3 series of experiments. In the first series samples of freshly dug potatoes were collected and cut lengthwise into two equal parts. One set of the samples was used immediately for the determinations of moisture, sugar, and starch. The corresponding halves were divided into 3 sets and each set stored at a different temperature for 12 days before similar determinations were made. The samples were stored at 30, 15.5, and 5° C. For a check a number of whole potatoes were subjected to the same conditions. The second series was a duplicate of the first, except that the potatoes were dug about 2 weeks later. This series would show any change occurring in the growing potatoes after the first series was harvested. The third series of experiments was modified so as to determine the effect of removal of the vines on the carbohydrate transformations. The roots were not harvested until 10 days after a killing frost.

HASSELBRING and HAWKINS pointed out that to the rate of carbohydrate transformations in stored sweet potatoes the Van't Hoff temperature law was applicable. In general, at 30° C. starch hydrolysis was rapid at first and soon reached an end point. At 15.5 C. a more normal rate of transformation took place, tending toward a state of completion. The hydrolysis at 5° C. was markedly retarded. In spite of the utilization of reducing sugar in respiration, HASSELBRING and HAWKINS were able to show a marked accumulation at first and very little subsequent accumulation. The concentration of the reducing sugar was found to be comparatively low during the period of storage. There was a lag in accumulation of cane sugar, associated with the increase of reducing sugar. The data suggested that the mode of carbohydrate transformation in stored sweet potatoes was from starch to reducing sugar, which resulted in the formation of cane sugar as the end product. On studying the effect of the vines on transformations, it was found that during their activity the sugar content remained low. As soon as the flow of materials was checked by removal of the vines, the usual transformations as found in storage of sweet potatoes manifested themselves.

HASSELBRING and HAWKINS[11] have pointed out that the internal changes during storage must play an important rôle in susceptibility to decay. Aside from the theoretical significance, it seems that this mode of attack on storage problems of this nature will be of economic value.—FRED W. GEISE.

Taxonomic notes.—BRITTON,[12] in continuation of his studies of West Indian plants, has described new species in *Cleome*, *Chamaecrista* (3), *Leucocroton* (3), *Passiflora* (3), *Rondeletia* (10), *Eriocaulon* (3), *Dupatya*, *Pilea*, *Ichthyomethia*, *Castelaria*, and *Stenostomum* (2).

[11] HASSELBRING, H., AND HAWKINS, L. A., Physiological changes in sweet potatoes during storage. Jour. Agric. Research **3**:331–342. 1915.

[12] BRITTON, N. L., Studies of West Indian plants. IX. Bull. Torr. Bot. Club **44**:1–37. 1917.

FAWCETT and RENDLE[13] have described new species of *Tephrosia*, *Cassia*, and *Erythroxylum* from Jamaica.

GATES[14] has described a new species of *Oenothera* (*O. novae-scotiae*) from Nova Scotia. It is related to *O. muricata*, but is distinct in leaf, stem, and bud characters, especially as to pigments. The species was studied in connection with the germination of 1000 of its seeds.

GREENMAN,[15] in continuation of his studies of *Senecio*, has presented § AUREI. The section includes 48 species, 5 of which are new, the descriptions being accompanied by a full bibliography and liberal citations of exsiccatae, especially such as occur in American herbaria. The same author[16] has also described a new vinelike *Senecio* (*S. Hollickii*) from Jamaica, collected by BRITTON and HOLLICK in 1908.

Miss HILL[17] has described a new species of *Spirogyra* collected in the basin of an old fountain in Seattle, Wash. It is named *S. gigantica* on account of its size, the filaments being 173–188 μ in diameter, the cells being 1–2 diameters long, and with 4–6 chloroplasts. It most nearly resembles *S. crassa*.

HUBBARD[18] has described a new species of *Agropyron* (*A. acadiense*) from Cape Breton, Nova Scotia, related to *A. Smithii* Rydb.

NAKAI,[19] in continuation of his studies of the plants of Japan and Corea, has described 15 new species in several genera, and proposes the following new genera: *Pentactina* (Spiraeaceae) and *Polakiastrum* (Scrophulariaceae).

OLIVE and WHETZEL,[20] in connection with a study of the parasitic fungi of Porto Rico, describe *Botryorhiza* and *Endophylloides* as new genera, and also 4 species of *Endophyllum* as new combinations, formerly referred to *Aecidium*.

PRAEGER,[21] in the course of a revision of *Sedum* as found in cultivation, has described 8 new species.—J. M. C.

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[13] FAWCETT, W., and RENDLE, A. B., Notes on Jamaica plants. Jour. Botany **55**:35–38. 1917.

[14] GATES, R. R., A new evening primrose. Trans. Nova Scotia Inst. Sci. **14**:141–145. *figs. 2*. 1916.

[15] GREENMAN, J. M., Monograph of the North and Central American species of the genus *Senecio*. Part II. Ann. Mo. Bot. Gard. **3**:85–194. *pls. 3–5*. 1916.

[16] ———, A new *Senecio* from Jamaica. Ann. Mo. Bot. Gard. **3**:201, 202. 1916.

[17] HILL, GRACE A., *Spirogyra gigantica*, n.sp. Puget Sound Marine Sta. Publ. **1**:198. *figs. 2*. 1916.

[18] HUBBARD, F. TRACY, A new *Agropyron* from Cape Breton. Rhodora **19**:15–17. 1917.

[19] NAKAI, TAKENOSHIN, Notulae ad plantas Japaniae et Coreae. XIII. Bot. Mag. Tokyo **31**:3–30. 1917.

[20] OLIVE, E. W., and WHETZEL, H. H., *Endophyllum*-like rusts of Porto Rico. Amer. Jour. Bot. **1**:44–52. *pls. 1–3*. 1917.

[21] PRAEGER, R. LLOYD, Some new species of *Sedum*. Jour. Botany **55**:38–44. 1917.

Enzyme activity of fungi.—With a view of ascertaining the manner of destruction of wood by *Lenzites saepiaria*, ZELLER[22] has made a general study of the enzymes in the mycelium and sporophores of that fungus. Enzyme preparations of the mycelium were made by extraction of dried and ground cultures of the fungus grown on sawdust. The enzyme mixture precipitated from the extract by means of alcohol was collected on filter paper and preserved dry. Preparations from the fruit bodies were made in a similar manner. From the activities exhibited by the powder thus obtained, the author concludes that the following groups of enzymes are present in the mycelium and sporophores of *Lenzites saepiaria:* (1) of the esterases chiefly those affecting the hydrolysis of the esters of the lower fatty acids; (2) of the carbohydrases, maltase, invertase, raffinase, diastase, innulase, ligninase (by which the author designates CZAPEK'S "hadromase"), cellulase, hemicellulase, and pectinase; (3) of other enzymes, emulsin, tannase, urease, hippuricase, nuclease, proteinases, rennetase, oxidase, and catalase.

It is of interest to note that in cultures of the fungus on resin agar emulsions containing a gradually increasing percentage of resin, growth was only slightly depressed in emulsions containing up to 50 per cent of resin. In emulsions containing over 50 per cent of resin growth is sharply depressed, while in those containing over 85 per cent growth is practically inhibited.—H. HASSELBRING.

Texas root rot.—DUGGAR[23] reports the finding of a conidial stage of the Texas root rot fungus, *Ozonium omnivorum* Shear, one of the most destructive fungous diseases of the cotton crop. The conidia-bearing hyphae usually occur in patches on the bare ground between the rows of plants and only rarely in connection with the roots themselves. They are borne on swollen or club-shaped branches recalling the conidiophores of some species of *Botrytis*. The spore powder which covers the ground of the fertile patches is pinkish buff. The fungus is tentatively placed in the hyphomycete genus *Phymatotrichum* as *P. omnivorum* (Shear) Duggar.—H. HASSELBRING.

Vegetation of Long Island.—HARPER[24] has published a list of the plants found growing on a part of Long Island which is really within the limits of New York City. It will serve for comparison with adjacent areas and as a record of the natural vegetation of an area which may soon become in reality a part of a densely populated city.—GEO. D. FULLER.

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[22] ZELLER, S. M., Studies in the physiology of the fungi. II. *Lenzites saepiari* Fries, with special reference to enzyme activity. Ann. Mo. Bot. Gard. **3**:430–512. *pls. 2*. 1916.

[23] DUGGAR, B. M., The Texas root rot fungus and its conidial stage. Ann. Mo. Bot. Gard. **3**:11–23. 1916.

[24] HARPER, R. M., The natural vegetation of western Long Island south of the terminal moraine. Torreya **17**:1–13. 1917.